Recovery of mature forest microclimate and bryophyte communities in logged forests

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Declaration

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Abstract

Globally, many forest ecosystems that undergo harvesting are adapted to natural disturbances such as fire. However, harvested forests can have depleted biodiversity due to different ecological impacts between harvesting and natural disturbance. To minimise the ecological changes due to forest harvesting, management techniques have been developed that better mimic the effects of natural disturbance. These techniques focus on retaining structural components of the pre-disturbance forest within harvested areas. Retained structures create more mature environmental conditions within the harvested area; these mature conditions encourage recolonisation and development of mature communities. Aggregated retention is an example of a management technique that retains mature forest elements. It involves the retention of patches (aggregates) of trees within harvested units. Retained aggregates have multiple benefits; they provide areas for mature forest species to persist through the disturbance period ("lifeboating"), and they can create more mature forest like conditions within the harvested area through "forest influence" – edge effects that occur within disturbed forest due to proximity to a nearby standing mature forest. Forest influence works through mechanisms such as shading and the reduction of dispersal distance.

Aggregated retention and other similar techniques have been implemented across many forest systems throughout the world. However, little is known about how effective they are for various groups of organisms. In Tasmanian forests, aggregated retention has been identified as an effective harvesting method for sustainable harvesting, yet information on how forest influence impacts environmental conditions and community structure is limited. Gaining knowledge on how increasing environmental maturity and the ways in which forest influence can aid in the return of pre-disturbance biological communities is crucial in the adaptive management of retention harvesting systems both in Tasmania and globally.

In this thesis, I investigate the impacts of forest influence on important abiotic components, specifically microclimate. I then assess the benefits of increased environmental maturity on recolonisation of bryophyte flora and the role that forest influence can have in bryophyte recolonisation. These topics are addressed across four experimental chapters. The first experimental chapter investigates how environmental conditions within harvested forest impacts on the level of maturity of bryophyte communities (Chapter 2). This is achieved by creating a measure of bryophyte community maturity within harvested forest. Various

environmental conditions were then tested to see if they impact the recolonisation of mature bryophyte flora.

Following on from this, I investigate whether distance from a mature forest edge (forest influence) can adjust the microclimate of disturbed forests (Chapter 3). Patterns in forest influence on bryophyte communities are then investigated (Chapter 4) to determine whether plots closer to a mature forest edge experience more rapid recolonisation by bryophytes. These questions are tested by sampling microclimate and bryophyte community composition across mature forest/harvested edges and analysing how condition change with distance from an edge. Additionally, as restoration of harvested areas is highly dependent on successional processes, the benefits of increased maturity and forest influence need to be assessed through time. Consequently, Chapters 2 - 4 were based on a chronosequence (space for time) study of sites that were previously clearfelled, to enable temporal impacts to be assessed. Finally, this thesis examines whether isolated aggregates generate the same level of microclimatic forest influence as the forest bordering the harvested area (Chapter 5). This comparison will help determine whether aggregated retention silviculture is an effective technique in generating environmental maturity within harvested forest.

Results of the thesis showed that mature environmental conditions within harvested areas did increase the maturity of bryophyte community compositions. Microclimate conditions were shown to be of particular importance in determining the community maturity of bryophytes within harvested forest. Results from Chapter 3 then showed that forest influence is an ecological process that can create mature forest microclimate conditions. Areas next to a mature forest edge experienced microclimatic conditions that were more similar to mature forest conditions within harvested areas. As well as its impact on microclimate, Chapter 4 showed that forest influence also impacted bryophyte communities. Bryophyte communities recover quicker in areas next to an edge compared to areas further away. In the final experimental chapter (Chapter 5), results showed that aggregated retention is an effective method to create microclimate forest influence within harvested areas.

Overall, I have shown that forest influence is effective at creating mature forest conditions within regenerating harvested forest, and that bryophyte recolonisation is aided by increased environmental maturity. This information can be used to refine management techniques, such as aggregated retention, which are designed to encourage forest influence for facilitating the successful restoration of harvested areas. The temporal response to forest

influence and the development of mature environmental conditions shows that future studies on the benefits of retention forestry should consider time since disturbance when reporting results.

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Chapter 1.
General Introduction

1.1. Background

Globally, forest disturbance is becoming an increasingly common occurrence (Hansen *et al.*, 2013). This has significant impacts on both landscape-level and local ecosystem processes and biodiversity (Marshall, 2000; McRae *et al.*, 2001; Fearnside, 2005; Zwolak, 2009). Given forest harvesting for silvicultural purposes is an important component of global forest degradation (Hansen *et al.*, 2013), forest managers are increasingly considering techniques that help preserve landscape-level ecosystem function and biodiversity. Whilst forests reserves play an important role in maintaining biodiversity within the landscape, effective conservation also needs to address management practices within harvested areas (Bengtsson *et al.*, 2003; Bauhus *et al.*, 2009). Therefore, harvesting techniques that aim to improve the chances of forest species to either survive or recolonise after disturbance can assist this effort.

With modern management techniques aiming to improve the chances of forest species to either survive or recolonise after disturbance, it is important to examine the responses of both flora and fauna to determine the effectiveness of these techniques. Bryophytes are an excellent group to study when examining the conservation-effectiveness of harvesting techniques, as most bryophytes, especially those commonly found within mature forests, are sensitive to both mechanical disturbance and to changes in microclimate conditions (Åström *et al.*, 2005; Dynesius and Hylander, 2007). This sensitivity commonly results in a high community turnover following disturbance (Caners *et al.*, 2013a; Kantvilas *et al.*, 2015), and among other factors, the return of pre-disturbance communities relies on the creation of appropriate environmental conditions and the ability of mature forest species to disperse back to the disturbed area. Many of the harvesting techniques that focus on maintaining biodiversity attempt to recreate appropriate environmental conditions that allow recolonisation, as well as maintaining some connectivity throughout the landscape. Retention forestry is one such technique; it can involve the creation of appropriate environmental conditions by leaving living trees within the harvested area. Given the aims of retention forestry, bryophytes are likely to be extremely responsive to such techniques. Bryophytes are vital indicators of functioning forest ecosystem (Frego, 2007): they provide critical ecosystem

services (DeLuca *et al.*, 2002; Lindo and Gonzalez, 2010), and can be used to predict appropriate environmental conditions (Batke *et al.*, 2015).

Clearfell burn and sow harvesting (clearfelling) is the dominant method of silviculture in Tasmanian wet forests. With this system, all trees are removed and after harvesting the remaining debris is burnt in very intense regeneration burns. This creates a seed bed for the eucalypt regeneration. However, in the past decade, harvesting using "aggregated retention" (where groups of trees are left within the harvested area) has begun to be used in some sites to improve biodiversity outcomes (Baker *et al.*, 2013a). In Tasmanian wet forests, aggregated retention silviculture involves a high intensity regeneration burn of the harvested area (although the fire is typically cooler than in clearfell burn and sow methods), but the retention areas remain unburnt, apart from occasional fire escapes. Whilst aggregated retention has numerous demonstrated benefits for biodiversity in Tasmanian wet forests (Gates *et al.*, 2009; Baker *et al.*, 2015; Fountain-Jones *et al.*, 2015), the drivers of these benefits remained poorly understood.

Understanding edge effects, such as forest influence, can also further develop ideas and concepts on community assembly processes. The ways in which communities assemble are known to impact ongoing ecosystem function (Fukami *et al.*, 2010) so that impacts of edge effects on initial recolonisation may have persistent follow-on impacts. Additionally, diversity of communities can be impacted by the scale and frequency of disturbance (Connell, 1978) and the composition of the surrounding species pool (Cornell and Harrison, 2014). By examining the succession of bryophyte communities following disturbance, this thesis aims to contribute to the understanding of general community succession following forest harvesting.

Overall this thesis aims to examine the role of forest influence in the regeneration of pre-disturbance conditions and communities. The benefits of forest influence are examined in the harvested wet eucalypt forest of Tasmania. Particularly, this thesis focuses on microclimate as a driver of forest influence and how forest influence impacts on bryophyte recolonisation of disturbed areas. This introductory chapter outlines the development of disturbance emulation forestry techniques, including aggregated retention, which is the preferred "new forestry" method in Tasmanian wet forests. As one of the main benefits of aggregated retention is the creation of edge effects within harvested areas (termed "forest influence"), this chapter will then discuss the potential benefits that forest influence can have on both

environmental conditions and on bryophyte communities of disturbed forests. Finally, the impacts that forest succession and other temporal dynamics can have on forest influence will be introduced.

1.2. Disturbance emulation forestry

Many forest systems used for timber harvesting are adapted to natural disturbances, such as fire or wind. Natural disturbances are common in harvested systems such as Northern Hemisphere conifer forests (Kuuluvainen, 2002; Long, 2009) and, the subject of this thesis, the eucalypt forests of Australia (Attiwill, 1994). Tasmania's mixed forests (those with both *Eucalyptus* and rainforest components) generally occur in areas where disturbances by fire are common (Gilbert, 1959). Traditional harvesting techniques such as clearfelling aim to emulate natural disturbances in these locations.

However, comparison of forests that have undergone natural disturbance and those that have undergone forest harvesting (through techniques such as clearfelling) shows that the disturbance type (i.e. natural or harvested) results in key ecosystem differences. For example, the quantity and quality of structural features such as living, dead, fallen and uprooted trees is greater in naturally-disturbed forests, but reduced or non-existent after harvesting (Andersson and Hytteborn, 1991; Siitonen *et al.*, 2000; Franklin *et al.*, 2002; Pedlar *et al.*, 2002). The retention of structures and increased patchiness in naturally-disturbed forests also reduces the extreme microclimatic conditions associated with traditional timber harvesting (Nitschke, 2005). These differences between disturbance types have been shown to have significant impacts on community compositions across a variety of taxa; e.g. fungi (Robinson and Williams, 2011), vascular plants (McRae *et al.*, 2001; Haeussler and Bergeron, 2004), bryophytes (Andersson and Hytteborn, 1991; Turner and Kirkpatrick, 2009; Yan *et al.*, 2013), vertebrates (Thompson *et al.*, 2003), and invertebrates (Chaundy-Smart *et al.*, 2012)(for a detailed list of studies see Kuuluvainen and Grenfell (2012)).

Understanding that techniques such as clearfelling result in forests that differ from their naturally-disturbed counterparts has led to the development of harvesting techniques which aim to increase mature forest structures/conditions within harvested forests. These harvesting methods aim to create disturbed forest which can undergo regeneration processes similar to those in natural systems, and ultimately return the forest to pre-disturbance conditions (Franklin, 1989; Lindenmayer and McCarthy, 2002). A variety of different techniques and terms have been developed including; continuous cover forestry

(Pommerening and Murphy, 2004); near natural forestry; close to nature forestry; and disturbance emulation forestry (Kuuluvainen and Grenfell, 2012). These techniques all centre on the retention of mature forest conditions within harvested landscapes. Increasing environmental maturity within harvested forests has proven to be successful at reducing negative impacts on community composition and species biodiversity (Rudolphi *et al.*, 2014; Hofmeister *et al.*, 2015).

1.2.1. Variable retention forestry

Variable retention (alternatively "green tree retention" or "retention forestry") is a harvesting method where residual trees are left within the harvested area for the duration of the prescribed rotation period (Franklin *et al.*, 1997; Vanha-Majamaa and Jalonen, 2001; Gustafsson *et al.*, 2012). Retained structures emulate patterns following natural disturbances, such as fire, which usually leave unburnt patches of trees within disturbed areas (Vanha-Majamaa and Jalonen, 2001).

When discussing the benefits of variable retention forestry, Franklin *et al* (1997) identified the main goals as:

1) "lifeboating" of species and processes;
2) enrichment of harvested areas with structural; and
3) enhancement of connectivity within the landscape.

By implementing harvesting techniques to achieve these goals, variable retention forestry not only supports higher survival ("lifeboating") of biodiversity within harvested areas, but also, encourages the subsequent reassembly of pre-harvest communities by aiding recolonisation. Recolonisation is aided by both the lifeboating of species, which reduces dispersal distances, and the retention of structural elements creating abiotic conditions within harvested areas more akin to mature forest conditions. Appropriate abiotic conditions such as microclimate have long been known to impact the species composition of understorey ecosystems (Geiger, 1950) and therefore environments more similar to mature forest are likely to be more amenable for the recolonisation of pre-disturbance communities. The two main approaches to variable retention currently employed worldwide are: group/aggregated retention (groups of trees large enough to protect understorey vegetation) (Fig. 1.1a) and dispersed retention (individual or small groups of trees) (Fig 1.1b) (Mitchell and Beese, 2002). In some areas, the two approaches are combined as mixed retention.

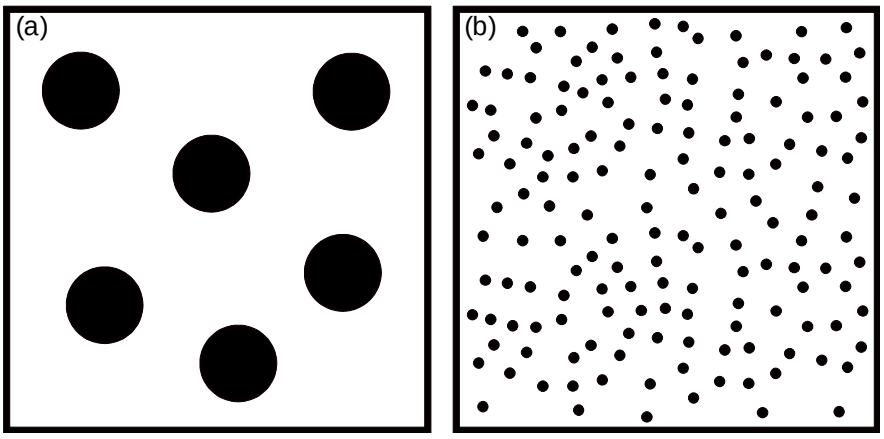

Fig 1.1: The two main forms of variable retention silviculture (demonstrated at 15% retention). (a) "Aggregated retention", large groups are retained for the duration of the rotation; and, (b) "Dispersed retention", small groups/individual trees are retained.

In order to determine the most effective alternative to clearfelling in Tasmanian wet forests, a Silvicultural Systems Trial was established (Hickey *et al.*, 2001). Results from this trial determined that aggregated retention was the best method of retention silviculture for wet eucalypt forests (Hickey *et al.*, 2015). Whilst dispersed retention was shown to be a dangerous method to implement in Tasmanian wet forests due to the increased risk of tree/limb fall (Hickey *et al.*, 2006; Neyland *et al.*, 2009), aggregated retention was selected as the safest alternative to clearfelling, but also provided the best ecological outcomes (Baker and Read, 2011). Aggregated retention has been shown to support the "lifeboating" of a range of taxa that are disadvantaged by recently harvested forest both in Tasmania and globally; examples of taxa that benefit include fungi (Gates *et al.*, 2009); rodents (Stephens *et al.*, 2012); insects (Pinzon *et al.*, 2012); vascular plants (Mori and Kitagawa, 2014); and bryophytes (Halpern *et al.*, 2012). Aggregated retention also retains mature environmental conditions (Soler *et al.*, 2015) this allows species to persist and then act as dispersal centres providing dispersal units to recolonise the harvested area. Aggregated retention also fulfils the second goal of variable retention by retaining structural features within the harvested area, and can create mature forest conditions within the harvested area through "forest influence", further aiding the recolonisation of pre-disturbance communities.

1.3. Forest influence

"Forest influence" is the term given to the edge effects that occur within disturbed forests due to proximity to a standing forest (Keenan and Kimmins, 1993) (Fig. 1.2). This direction

of edge effects is often understudied compared to the commonly examined interior forest edge effects, yet in some circumstances can induce more substantial impacts (Alignier *et al.*, 2014). Research on interior edge effects are highly beneficial and provide critical information for the conservation of forest fragments (Murcia, 1995); however, forest influence is an equally important concept as it can be incorporated into the restoration of disturbed forests by forest managers (Baker *et al.*, 2013a).

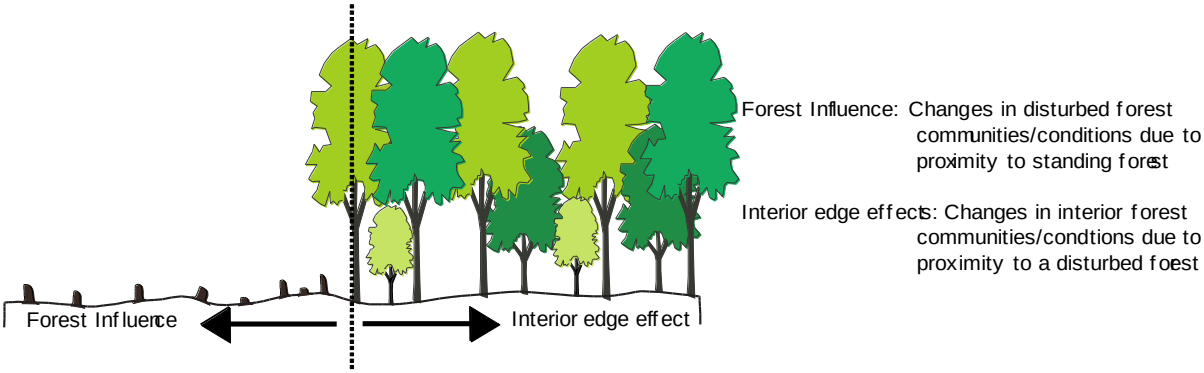

Fig 1.2: The direction and definitions of edge effects that occur at the interface between mature and disturbed forests. Dotted line represents the boundary (edge) between the two forest types.

Forest influence impacts biological process such as dispersal distance (Fig. 1.3c), as well as the physical characteristics of the disturbed forest such as microclimate (Fig. 1.3a, b) (Mitchell and Beese, 2002; Beese *et al.*, 2003). By impacting these aspects, forest influence can effect community composition by facilitating the recolonisation of mature forest species, particularly near an edge. Therefore, two approaches can be taken with the study of forest influence; firstly on the drivers of forest influence, and secondly on the response of communities or individual species' to forest influence.

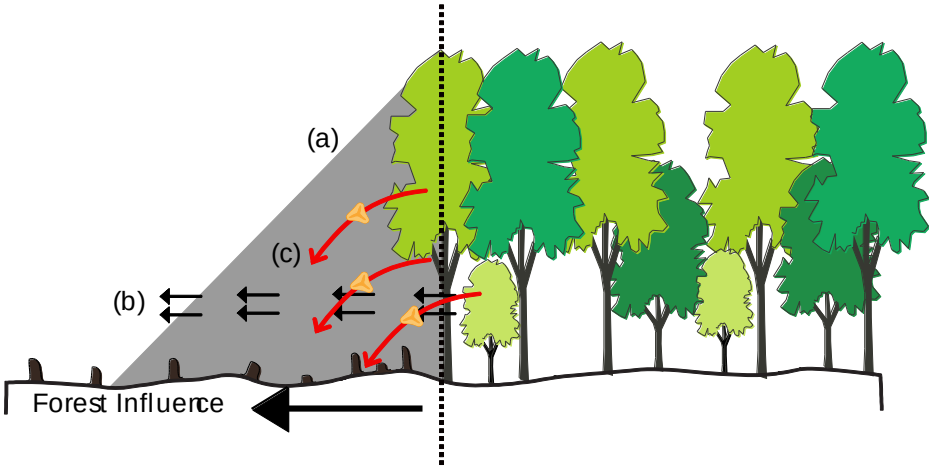

Fig 1.3: Potential drivers of forest influence. (a) Shading of disturbed forests by standing forests. (b) Flow of air from standing forests into disturbed forest. (c) Dispersal of propagules from sources within the standing forest. Figure adapted from (Baker *et al.,* 2013a).

As mentioned, aggregated retention is suggested as an effective approach to increase the amount of forest influence within harvested areas (Franklin *et al.*, 1997; Mitchell and Beese, 2002). Current guidelines for implementing aggregated retention in some regions, including Tasmania, state that the majority of the harvested area should be within one tree height of the standing forest (Mitchell and Beese, 2002; Baker and Read, 2011), as this distance is the present rule-of-thumb used to estimate the operating distance of forest influence (Keenan and Kimmins, 1993; Mitchell and Beese, 2002; Baker *et al.*, 2013a). While recent evidence has suggested that this estimation can be effective for a variety of components e.g. bryophytes (Baker *et al.*, 2013b); beetles (Fountain-Jones *et al.*, 2015); and abiotic variables (Heithecker and Halpern, 2007), other studies have shown responses which do not match the one tree height estimation (see Baker *et al*. (2013*a*) for review). It is imperative that more study is undertaken to determine how communities respond to forest influence and what factors might drive variation in their responses. Furthermore, investigating the driving factors and community responses will allow for the optimisation of the current operational guidelines of aggregated retention.

1.3.1. Forest influence on microclimate

Forest disturbance creates microclimate conditions that are unlike the conditions of undisturbed forests (Zheng *et al.*, 2000; Aubury *et al.*, 2009). In particular, disturbed forest microclimate is much more variable (Chen *et al.*, 1993) resulting in higher maximums and lower minimums. This can impact community compositions as many species occurring in mature forests prefer stable microclimate conditions (Motzkin *et al.*, 2002; Welsh Jr *et al.*,

2007). However, microclimatic conditions are not just determined by forest type; interior edge effects have significant impacts on the microclimate conditions within standing forests (Matlack, 1993; Chen *et al.*, 1995; Gehlhausen *et al.*, 2000). While not studied to the extent of interior edge effects, forest influence has also been shown to impact the microclimate of forests regenerating after disturbance (Young and Mitchell, 1994; Huggard and Vyse, 2002; Redding *et al.*, 2003; Godefroid *et al.*, 2006; Heithecker and Halpern, 2007). In Tasmanian forest systems, the extent to which forest influence effects the microclimate of regenerating forests has never been determined; however it is important that these effect be considered, as microclimate gradients created by edge effects can have significant effects on forest biota (Gehlhausen *et al.*, 2000), and as such, can inform forest management practices.

Whilst some studies have shown that microclimatic forest influence occurs, the drivers of forest influence have only been discussed not tested. Some studies suggest that shading of disturbed forests by standing trees is a strong driver of forest influence on microclimate (Young and Mitchell, 1994; Cadenasso *et al.*, 2003; Godefroid *et al.*, 2006) (Fig 1.3a) and transmitted light has been shown to respond to distance from a standing forest edge (Huggard and Vyse, 2002; Heithecker and Halpern, 2007). However, Godefroid *et al.* (2006) reported that in European beech forests, microclimate was adjusted past the point of shading and suggested that the flow of air from one forest type to another could be responsible (Fig 1.3b). The importance of factors such as shade can be examined by testing the strength of microclimatic forest influence with changes in environmental conditions such as cloud cover and precipitation. These environmental factors reduce the amount of sunlight reaching the forest floor (Yang *et al.*, 2012), thus may reduce the impact of shade. Additionally, as the depth of shade is known to be driven by the height of standing forest, solar altitude, site slope and the direction of the mature forest (Ozdemir, 2008), the theoretical depth of shade can be calculated and compared to the depth of forest influence. Determining the importance of these two factors is difficult, as they are both expected to produce similar gradients. In addition, the relative importance may change with the development of canopy cover in the disturbed forest (see "Temporal patterns in forest influence" below).

Of the limited studies focusing on microclimatic forest influence, the majority examine edges which are connected to a large area of standing forest or are at the edges of harvested coupes, e.g. (Young and Mitchell, 1994; Huggard and Vyse, 2002; Redding *et al.*, 2003; Dovčiak and Brown, 2014). To date, only Heithecker and Halpern (2007) have examined microclimatic forest influence generated by retained aggregates. However, no studies have

examined the levels of forest influence generated from aggregates in comparison to forest influence generated from larger areas of mature forest that are commonly adjacent to harvested areas. There are likely to be differences in the level of forest influence for these two edge types, as a greater proportion of an aggregate is expected to experience interior edge effects (Laurance and Yensen, 1991; Didham and Ewers, 2012), meaning the microclimatic conditions available to diffuse into the disturbed forests may be less "mature". Additionally, the penetration of sunlight around the periphery of an aggregate will mean the disturbed forest is shaded for a smaller period of time than areas near the larger forest that surround harvested areas. As the biodiversity benefits of aggregated retention are based on the premise that it will aid recolonisation by altering environmental conditions, knowing how effective retained aggregates are in generating forest influence is crucial and requires further examination.

1.3.2. Forest influence on species

Community composition of flora and fauna are also known to exhibit patterns within harvested forests due to proximity to a standing forest edge. Increased recolonisation of disturbed forests close to a mature forest have been observed for beetles (Fountain-Jones *et al.*, 2015), fungi (Gates *et al.*, 2009), bryophytes (Baker *et al.*, 2013b) and vascular plants in Tasmanian forests (Tabor *et al.*, 2007) and overseas (Outerbridge and Trofymow, 2009; Baker *et al.*, 2015). Although it should be noted that some taxa, such as birds (Hingston *et al.*, 2014), show gradients of forest influence at harvesting scales (cut block). Patterns in the biota due to forest influence are likely due to species responses to changes in abiotic conditions, such as microclimate (see above). The recolonisation, growth and survival of many species are highly responsive to microclimate changes (Battaglia and Sands, 1997; Renhorn *et al.*, 1997; Grimbacher *et al.*, 2006). For example, a number of studies of interior edge effects have identified microclimate as a major driver of the observed gradients in community composition (Didham *et al.*, 1998; Gehlhausen *et al.*, 2000; Stewart and Mallik, 2006; Magnago *et al.*, 2015). This is also likely to be the case for biotic patterns due to forest influence (Dovčiak and Brown, 2014).

As well as responses to abiotic gradients, biotic gradients due to forest influence can result from a reduction in dispersal distances due to increased proximity to a mature forest edge (Fig 1.3c). Propagule dispersal patterns are known to be highly leptokurtic in bryophytes (Laaka-Lindberg *et al.*, 2003; Pohjamo *et al.*, 2006) and reduction in vascular plant seed deposition has been noted in association with increased distance from a forest edge

(Vespa *et al.*, 2014). Dispersal distance has been shown to limit species recolonisation in recovering old-fields (Cramer *et al.*, 2008) and for forests (Moir *et al.*, 2005; Sagnard *et al.*, 2007); although, these studies note that dispersal distance is often combined with other environmental limitations. The effect of forest influence on community compositions is likely to be driven by a combination of dispersal limitations and more mature environmental conditions close to a forest edge. Gathering more information on which factors drive patterns in forest influence will enable management techniques which rely on this process to be refined.

1.3.3. Forest influence on bryophytes

Given that dispersal limitations and increased environmental maturity close to a mature forest edge are thought to be the main factors driving forest influence, bryophyte communities should be a very responsive group. Bryophytes are very sensitive to microclimatic conditions within forests (Busby *et al.*, 1978; Hylander *et al.*, 2002; Wiklund and Rydin, 2004b). Indeed, patterns in bryophyte growth have been shown to match with gradients in microclimate conditions (Stewart and Mallik, 2006). It is therefore expected that microclimate patterns associated with forest influence would result in changes in establishment and growth rates of bryophytes. Additionally, many bryophytes, especially mature forest species, are known to be dispersal limited (During, 1979). This is particularly prevalent in species which rely on dispersal by asexual propagules (Kimmerer, 1994).

Results of previous studies investigating changes in bryophyte community composition with distance to mature edge have been mixed; some studies detect relationships (Caruso *et al.*, 2011; Baker *et al.*, 2013b), yet a study by Hylander (2009) showed no response. Many factors cause variation in the response to edge effects; slope and aspect alter the severity of edge effects on abiotic conditions (Heithecker and Halpern, 2007) and this can have flow on effects to the community responses including those of bryophytes (Hylander, 2005). Additionally, the strength of interior edge effects is determined by the type of disturbance that the forest is adjacent to (Mesquita *et al.*, 1999). Likewise, the scale of forest influence is likely determined by the nature of the standing forest adjacent to the harvested area. It is therefore important to gain an understanding of the role of forest influence for multiple forest types. Prior to this thesis, only a single study (Baker *et al.*, 2013b) had examined forest influence on bryophytes in temperate eucalypt forests and this was limited to a single site.

Bryophytes provide an excellent group to study the effects of forest influence as their biological characteristics means that the majority of species are highly sensitive to the environmental changes associated with forest harvesting. For example availability of moisture is a key determinant of bryophyte function (Gundale *et al.*, 2009) and also has a strong role in spore germination (Wiklund and Rydin, 2004b). This sensitive to environmental change makes bryophytes an excellent indicator species (Brunialti *et al.*, 2010), especially for evaluating the effects of forest management (Hylander *et al.*, 2002).

1.4. Temporal patterns in forest influence

Interior edge effects are known to be temporally dynamic, and changes in the strength and depth of edge effects can occur over the course of the day (Chen *et al.*, 1995; Newmark, 2005), seasonally (Pohlman *et al.*, 2009), and with the age of the disturbed forests (Matlack, 1994; Dodonov *et al.*, 2013; Dupuch and Fortin, 2013). Temporal changes have important consequences for the types of species which may be impacted. For example, many species have important life history characteristics such as flowering, germination or mating which only occur during a single time of year. If this important life history event falls during a period when forest influence is low then the species may not be impacted at all. Therefore, it is important to consider temporal dynamics of forest influence. Temporal examination of forest influence has been touched on, with Davies-Colley *et al.* (2000) showing the impact on microclimate changes with daily environmental conditions, Saunders *et al.* (1999*)* showing changes over the day, Young and Mitchell (1994) showing differences between seasons and Dovčiak and Brown (2014) showing differences with time since disturbance. Only the study by Dovčiak and Brown (2014) examined temporal changes in anything other than microclimate. A literature survey did not reveal any studies detailing temporal changes in forest influence on bryophytes.

1.4.1. Forest Succession/edge contrasts

One of the main causes of temporal variability in forest influence may stem from changes in the level of contrast between disturbed and standing forests. Patch contrast refers to the difference between adjoining ecosystems (see Harper *et al.* (2005) for full definition). With interior edge effects, a reduction in patch contrast often leads to a reduction in the strength of the edge effect (Peyras *et al.*, 2013). As a forest regenerates after disturbance, the difference in both environmental conditions and community composition between the disturbed area and the retained mature forest will be reduced, and therefore the impact of

forest influence may also be reduced. Changes in the disturbed forest may also lead to changes in the drivers of forest influence; for instance canopy closure during forest regeneration may reduce the impact of shade on microclimatic forest influence. It is therefore important to consider time since disturbance and the successional stage of the disturbed forest when reporting on the impacts of forest influence.

1.4.2. Bryophyte Succession

Forest succession can also drive changes in bryophyte community composition due to changes in light and moisture characteristics of the disturbed forest (Fenton and Bergeron, 2006). Indeed, successional patterns in bryophyte communality composition follow well defined pathways as the forest ages after disturbance (Hodge *et al.*, 2009; Browning *et al.*, 2010). Like forest succession, bryophyte succession has the potential to alter the community response to forest influence. Species which colonise immediately after disturbance are generally adapted to have high dispersal abilities (During, 1979; Esposito *et al.*, 1999) and to be tolerant of a range of microclimatic conditions (During, 1979). Bryophyte species with good dispersal ability typically produce dust-like spores that can travel tens of kilometres (Rydin, 2009). Such species are unlikely to benefit substantially from closer propagule sources, which is major component of forest influence. However, bryophytes that occur at the later stages of succession are more likely to be dispersal-limited (During, 1979; Kimmerer, 1994), and their dispersal generally exhibits strong leptokurtic patterns (Laaka-Lindberg *et al.*, 2003; Pohjamo *et al.*, 2006) meaning that areas close to a propagule source (retained mature forest) will receive more propagules and have a higher chance of recolonisation. Mature forest bryophytes also tend to be more sensitive to microclimatic conditions (Busby *et al.*, 1978; Stewart and Mallik, 2006) due to growth form and sensitivity to damage from radiation, thus they will also benefit from the microclimatic changes induced by forest influence. Mature forest affiliated bryophytes have been shown to be more sensitive to interior edge effects (Löbel *et al.*, 2012), yet the change in responsiveness to forest influence with seral stage has not been previously detailed.

Whilst some bryophytes, particularly late seral species, may be dispersal-limited, temporal aspects of dispersal have to be taken into account, as bryophyte dispersal is a highly stochastic process (Fenton and Bergeron, 2013). While short term studies may suggest that species are dispersal-limited, longer time periods may reveal this not to be the case (Sundberg *et al.*, 2006). Therefore, forest influence patterns that are driven by dispersal limitations may not persist through time. Additionally, as the microclimatic contrasts between forest types

diminish with forest succession, the scale of microclimatic forest influence may diminish with time. Temporal changes in bryophyte responsiveness to forest influence are complex due to the temporal changes in life history characteristics, the strength of microclimatic forest influence, and the stochastic nature of bryophyte dispersal. It is therefore unsurprising that temporal dynamics of forest influence on community composition has never been investigated for bryophytes, and has only recently received attention in other taxa (Fountain-Jones *et al.*, 2015).

1.5. Aims

In this thesis I aim to:

1. Determine the key environmental variables within disturbed forests that impact on the recolonisation of pre-disturbance bryophyte communities.
2. Examine patterns in the microclimate of disturbed forests which are generated by adjacent standing forests (forest influence on microclimate).
3. Examine patterns in bryophyte communities within disturbed forest which are generated from distance to adjacent mature forest (forest influence on bryophytes).
4. Determine how forest influence on both microclimate and bryophyte communities changes with time (short to long time scales).
5. Test the difference in the scale of microclimatic forest influence which is created adjacent to retained aggregates compared to larger intact edges surrounding a harvested unit.

1.6. Overview of chapters

My thesis consists of six chapters. Chapter 3 has been published in the journal Forest Ecology and Management (Baker *et al.*, 2014). Chapter 4 is currently under review with the Journal of Vegetation Science. Chapter 5 is in under review with the Journal of Forest Ecology and Management and Chapter 5 has been written for publication and has been developed with the assistance of co-authors. My contributions and those of my co-authors are listed at the start of each chapter. In all chapters I was the lead author and developed the experiments and analysis with the help of co-authors. Publications have been modified slightly for inclusion into this thesis.

In Chapter 2, I develop a technique to measure the "maturity" of bryophyte community composition within harvested forests. Using this scale of bryophyte community maturity, I examine which environmental conditions are important in creating mature bryophyte communities within regenerating harvested forests.

In Chapter 3, I test the effect that distance to a mature forest edge has on microclimatic conditions within harvested forests. Microclimatic forest influence was examined across three age classes in order to detect changes associated with forest succession, and to see if forest influence persisted though time. In addition, this chapter considers changes in microclimatic forest influence across monthly and daily time periods.

In Chapter 4, I examine patterns in bryophyte community composition within harvested forest that are driven by distance to a mature forest edge. These patterns are examined over three age class of disturbed forests. Analysis focuses on how the depth and magnitude of forest influence change over time.

In Chapter 5, the ability of retained aggregates to generate microclimatic forest influence was compared to mature forest at the boundary of a harvested area. Microclimate conditions were examined throughout a year to see if there was a temporal trend in the difference between edge types. This approach also allowed conclusions to be drawn about how microclimatic forest influence is generated.

In Chapter 6 (the general discussion), the results from Chapters 2-5 are compiled to determine how the recolonisation of pre-disturbance bryophyte communities can be aided by retention forestry practices. The results from Chapters 3 and 5 are used to discuss how microclimatic forest influence is created and then compared discussed to see how retention practices can alter environmental conditions within harvested forests and thus enable the efficient recolonisation of pre-disturbance communities.

Plate 1. Examples of the forest structure at each of the three age classed of regeneration forest studied in chapters 2-4 in this thesis.

~7 years post-harvest

This age of forest was characterised by large areas of *Gahnia grandis* (as shown) and dispersed amongst thick *Eucalyptus* regrowth (as shown). In some of the ~7 year old sites, saplings of *Pomaderris apetala* were also prominent in the vegetation.

~27 years post-harvest

This age of forest was characterised high stem density, canopy closure and a low coverage of understorey vegetation. Species that were common in this age class included *Eucalyptus*, *Pomaderris apetala* and *Acacia dealbata.*

~45 years post-harvest

This age class was characterised by lower stem density as a result of self thinning. Higher ground coverage also occurred in this age class with the fern species *Dicksonia antarctica* and *Polystichum proliferum.* Species dominating the canopy level include *Eucalyptus, Pomaderris apetala* and *Acacia dealbata*.

Chapter 2.
Environmental drivers of bryophyte recolonisation

This manuscript had contributions from the following people:
Thomas P. Baker (candidate), Gregory J. Jordan, Nicholas M. Fountain-Jones, Jayne Balmer, Patrick J. Dalton and Susan C. Baker

This study was conceived of by TPB, SCB, and GJJ. TPB conducted the study, analysed the data and wrote the manuscript. JB and NF-J helped collect environmental data and set up field sites. PJD assisted candidate with species identification. Guidance and corrections of the manuscript were provided by SCB, GJJ, PJD and JB.

2.1. Abstract

The success of bryophytes recolonisation after disturbance is governed by both the environmental conditions found within disturbed forests and the distance over which species have to disperse. This chapter aimed to identify what environmental factors limit the re-establishment of pre-disturbance (mature forest) bryophyte communities following timber harvesting and whether the importance of environmental factors (including dispersal distance) varies depending on substrate.

Bryophyte composition was examined on four substrates (coarse woody debris, ground, rocks and exposed roots) within three age classes of harvested wet eucalypt forest (~7, ~27 and ~45 years post disturbance). Bryophyte community composition within harvested forest was compared to mature forest communities to determine their relative level of maturity using axis scores from one dimensional constrained ordinations. Bryophyte communities varied between substrates and their maturity level was found to be associated with several environmental factors. Microclimate conditions were particularly important in limiting re-establishment of mature bryophyte communities across all substrates. Whilst microclimate was the most dominant environmental predictor, substrate specific environmental factors contributed to predicting bryophyte community maturity within harvested forests, although the importance of factors changed with forest age.

The study findings have important implications for refining harvesting techniques which encourage bryophyte recolonisation through the retention of mature environmental conditions. This chapter shows that having microclimate conditions that resemble those in mature forests allows the recolonisation of a more mature bryophyte flora. This study also showed that temporal dynamics of bryophyte recolonisation need to be considered in future studies, as time since disturbance can impact the environmental drivers of recolonisation.

2.2. Introduction

Forest harvesting often results in different community compositions, of many taxa, compared to natural disturbances (McRae *et al.*, 2001; Thompson *et al.*, 2003). Specifically, this has been observed for bryophyte flora, both globally (Gustafsson and Hallingbäck, 1988; Hannerz and Hånell, 1997; Yan *et al.*, 2013) and in Tasmanian wet eucalypt forests (Turner and Kirkpatrick, 2009). Forest bryophyte communities are sensitive to disturbance by harvesting, as many species are killed by mechanical disturbance, or are eliminated following harvest due to their intolerance to the greater environmental extremes associated with

disturbed forests (Vanha-Majamaa *et al.*, 2007). In addition, fire, which is often used in the regeneration of eucalypt forests, kills the vast majority of the bryophyte flora (Pharo *et al.*, 2013). Survival of bryophytes within the harvested area is rare but does occur to some degree under logs and in wet gullies/depressions. Restoration of most forest bryophytes following disturbance therefore relies on successful recolonisation from beyond the disturbed area.

Recolonisation of disturbed forests by bryophytes is driven by two main factors: environmental conditions of the disturbed site and the distance to the nearest bryophyte propagule source. Many environmental factors impact the recolonisation of bryophytes. Vegetation cover and the associated microclimate conditions are key drivers of bryophyte community composition (Turner *et al.*, 2006; Coote *et al.*, 2013). Dispersal distance is often considered to only have a minor impact on bryophyte recolonisation (Hylander, 2009) compared to the impact of habitat quality (Werner and Gradstein, 2009), because the production of dust-like spores results in many bryophyte species being able to disperse over kilometres (Hutsemekers *et al.*, 2008; Rydin, 2009). Nevertheless, dispersal limitations have been shown to effect recolonisation of some bryophytes (Snäll *et al.*, 2004; Kimmerer, 2005), particularly mature forest species that rely on dispersal of larger asexual propagules (During, 1979). Larger propagules generally disperse over shorter distances (Söderström and During, 2005). Species that rarely produce sporophytes, or have large spores, are restricted in the recolonisation of harvested forests (Caners *et al.*, 2013b). Therefore, the restoration of post-harvest forests to pre-disturbance communities may be improved when recolonisation is not limited by dispersal distance.

Harvesting approaches that better emulate natural disturbances have been developed to reduce some of the negative impacts that are associated with traditional clearcutting harvesting methods (see Kuuluvainen and Grenfell (2012) for review). These retention forestry approaches focus on retaining mature forest species, structures and conditions within harvested areas (Franklin, 1989; Heithecker and Halpern, 2006; Bauhus *et al.*, 2009; Baker *et al.*, 2014). The maintenance of mature forest conditions and structures within harvested areas is expected to increase the rate and likelihood of recolonisation of mature forest species. Increased recolonisation in association with retention practices has been previously documented for a range of taxa (Fedrowitz *et al.*, 2014; Fountain-Jones *et al.*, 2015). A variety of retention forestry techniques have also been shown to aid the recolonisation of mature bryophyte communities (Nelson and Halpern, 2005b; Dovčiak *et al.*, 2006; Baker *et al.*, 2013b; Caners *et al.*, 2013a; Dovčiak and Brown, 2014). However, as the response of

individual taxa to retention harvesting is variable (Baker *et al.*, 2013a), the study of environmental factors most important in aiding the recolonisation of pre-disturbance bryophyte communities may be useful for improving retention forestry techniques.

The response of bryophytes to environmental conditions can vary due to the large number of substrates that bryophytes inhabit. For example, the degree of decay is an important factor influencing which species colonise coarse woody debris (Mills and Macdonald, 2005), and litter depth is likewise important in influencing the species present on the forest floor (Schmalholz and Granath, 2014). While many species can occur on multiple substrates (Tng *et al.*, 2009), many have preferences for, or are restricted to, a single substrate (Ódor and Standovár, 2002). Responses of the bryophyte community on each substrate type may therefore differ due to particular life history characteristics associated with each substrate. Thus it is important to know which environmental conditions impact bryophyte communities on various substrates, as managing for multiple substrates is important for maintaining high bryophyte diversity (Lõhmus *et al.*, 2007).

In addition to variability in response to environmental conditions across substrates, conditions in forests undergoing succession are temporally dynamic (Lebrija-Trejos *et al.*, 2011), so drivers of recolonisation may change with time. Furthermore, bryophyte communities also undergo successional changes (Schmalholz and Hylander, 2009; Browning *et al.*, 2010; Turner *et al.*, 2011); accordingly, different species are present depending on forest age. Bryophytes at different successional stages generally have different life history characteristics (Longton, 1997). Thus, an early seral bryophyte community may not respond to the same environmental factors as a late seral community. Studies that only focus on environmental conditions that aid bryophyte recolonisation at the initial stage of recolonisation may miss important environmental factors that impact species at the later stages of recolonisation. Furthermore, bryophyte dispersal and recolonisation is highly stochastic (Frego, 1996; Fenton and Bergeron, 2013), therefore responses to environmental predictors may need time to develop. Examining the temporal dynamics of bryophyte recolonisation may be able to show responses to environment more clearly.

This chapter examines bryophyte recolonisation within harvested forests by modelling bryophyte community composition against environmental conditions and distance to mature forest. It aims to determine which environmental predictors drive the maturity of the bryophyte community within the disturbed forest. A measure of community maturity (how

similar a community in the disturbed forest is to the pre-disturbance community) is developed to answer this overall question and the following sub-questions:

1) What environmental conditions, including distance from mature forest, are most associated with the recolonisation of mature bryophyte communities?
2) Do communities on different substrate types respond differently to environmental conditions or distance to mature forest?
3) Do environmental conditions most associated with bryophyte community maturity differ in relation to changes in forest age?

2.3. Methods

2.3.1. Study sites

Bryophyte community composition and environmental conditions were studied at twelve sites in Tasmania's southern forests, Australia (also used by Baker *et al.* (2014) and Fountain-Jones *et al.* (2015)) (Fig. 2.1a). All sites consisted of a harvested area occupied by forest regenerating following clearfell, burn and sow (CBS) silviculture. During CBS silviculture all trees in the area are removed and the debris is then set alight in a high-intensity regeneration burn. The combined clearing and burning process removes the vast majority of bryophyte flora, meaning bryophytes generally have to recolonise from the surrounding forest. Harvested sites were selected that shared a boundary with mature forest in which damage from escaped regeneration burns and wind throw was minimal. Another condition of site selection was that the adjacent mature forest patch was dominated by *Eucalyptus obliqua* and/or *E. regnans* and had an understory dominated by rainforest trees including *Nothofagus cunninghamii* and/or *Atherosperma moschatum* with other species such as *Eucryphia lucida*, *Phyllocladus aspleniifolius* and *Anodopetalum biglandulosum*. Prior to disturbance it was assumed that the harvested forest was floristically similar to the surrounding mature forest.

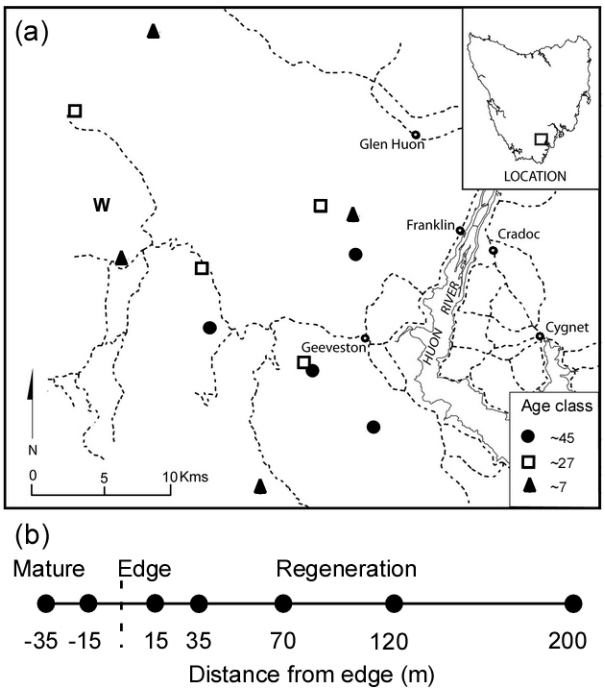

Figure 2.1: The study location and transect design used in the study. (a) Map of the southern forests showing the location and age of the twelve sites used in the study. (b) Transect design showing the location of study plots in relation to the mature forest boundary, three transects were used per site.

2.3.2. Experimental design

The study sites encompassed a chronosequence of forest regeneration ages, with four sites in each of three age class; "~7 year old regeneration forests" harvested between 2002 and 2007; "~27 year old regeneration forests" harvested between 1983 and 1989; and "~47 year old regeneration forests" harvested between 1966 and 1972 (Fig. 2.1a) (plate 1). Within each site, three parallel transects were established perpendicular to the mature forest edge, along which seven 10 x 10 m plots were located such that the first two plots were placed within the mature forest at -35 and -15 metres from the mature forest edge (- indicating a mature forest plot) and five plots were located in the harvested forest at 15, 35, 70, 120 and 200 metres from the mature forest edge (Fig. 2.1b). Edge location for each transect was pre selected based on maps of the harvested area and then adjusted on the ground so that it did not have any visible damage from fire or windthrow, plot locations were then determined by the distance from the edge. Two mature forest plots associated with the ~27 year old regeneration forest were excluded due to subsequent forest disturbance, resulting in a total of 250 plots being used for this study, of which 70 were within mature forests.

Plate 2: Images of the substrates sampled for bryophyte cover. Data collected from rocks, roots, CWD and ground substrates were used in Chapter 2. Data collected from ground and CWD was used in Chapter 4.

Root: Roots selected were exposed and living. Image shows the placement of the 10 x 10 cm quadrat used for sampling. The width of the root was also recorded. Image is taken form a ~27 year old forest

Ground: The ground substrate was sampled in areas where there was no coarse woody debris, rocks or roots present. This image was taken in a ~7 year old forest. Main species is *Polytrichum juniperinum* Hedw.

Rock: Rock substrates were sampled that were clear of any debris including fine scale leaf litter. The longest length of the rock was also recorded. Image is taken form a ~27 year old forest.

Coarse woody debris: Logs (CWD) were sampled that were over 10cm in diameter. Positioning on the log was determined by nearest point to the sample point. The width and decay class of the CWD piece were also recorded. Image is taken form a ~7 year old forest.

2.3.3. Bryophyte sampling

Bryophyte sampling occurred between January 2012 and May 2013. Within each plot, species cover was recorded on four different substrates; coarse woody debris (over 10 cm in diameter), exposed roots of living trees, rocks, and the ground (Plate 2). Species cover was recorded using five 10 cm x 10 cm quadrats per substrate per plot, this size was selected as it was the maximum size that could be surveyed consistently for all four substrates. To determine quadrat placement, the plot was divided into five segments. For each substrate type, a quadrat was placed on the closest available piece of substrate to the centre of the segment. If the segment did not have a particular substrate then the closest unsampled piece of substrate within the plot was used, and the segment was recorded as empty. As ground substrates were always present, empty segments were not recorded for this substrate type; however, the number of segments without bryophyte cover on the ground was noted and this was included in the total empty segments of the plot (Table 2.1). Quadrats without bryophyte cover were recorded as zero cover. At each plot, sampling continued until five quadrats with bryophytes present were recorded per substrate (or a maximum of 25 total quadrats per substrate). All species within a quadrat were identified to species level and given a percentage cover. Species were generally identified in the field but when this was not possible, lab-based identification occurred. Nomenclature and identification used published keys for specific genera although common species were identified using Scott (1985) for liverworts and Scott and Stone (1976) for mosses. All species were identified at the species level with the exceptions of the moss genus *Bryum* and the liverwort genera *Telaranea* and *Riccardia*, although *R. aequicellularis* and *R. cochleata* were identified to the species level. All species identified during sampling are listed in appendix 1.

2.3.4. Environmental predictors

At each plot, twenty-one environmental variables were recorded; these variables are detailed in Table 2.1. This data included both plot-level variables, which were measured at the centre of each plot and substrate-level variables which were collected for each quadrat placed, regardless of the presence of bryophytes. Three microclimate variables were also recorded, temperature, relative humidity and vapour pressure deficit (calculated from the direct measurements of temperature and relative humidity using methods in Allen (2005)). Relativity humidity was included as it gives an indication of the moisture available for the bryophytes, whereas vapour pressure deficit indicates the potential for water loss.

Table 2.1: List of the environmental predictors and the methods used to collect them. Plot variables were those recorded for the whole plot level (10 x10 m). Substrate variables were collected from a single substrate type ([1]ground, [2]rocks, [3]roots, [4]CWD). [*]Variables recorded only on the second transect, see Baker et al. (2014) for more details.

Plot variable	Substrate variable	Collection method
Leaf area index (LAI)		Recorded using hemispherical photography and calculated in GAP light Analyzer (Cary Institute of Ecosystem Studies, New York, USA)
Vegetation cover		Total estimated percentage projected foliage cover of vegetation in the 10 x 10 m area
Total empty segments		Sum of empty segments for each substrates plus the number of segments without bryophyte cover on the ground (0-20)
Heat load		Estimated irradiance that would be received under full sunlight with no vegetation cover. Calculated using plot aspect, slope and latitude based on McCune and Keon (2002)
Distance from edge		The distance of the plot to the mature forest edge
Tree diameter		Average diameter at breast height of the trees (above 10cm) in the plot.
	[1]Bare ground cover	Estimated percentage cover of ground not covered by litter, CWD, rock or ground vegetation
	[1]Litter cover	Estimated percentage cover of ground litter and fine woody debris (<10cm in diameter)
	[1]Litter depth	Average value of 6 litter depth measurements within the plot
	[2]Rock empty segments	Number of segments with no rock substrate available (0-5)
	[2]Rock cover	Estimated percentage cover of rocks
	[2]Rock size	Average size of the 5 selected rocks in each plot. Rock size was measured across the longest visible face
	[3]Root empty segments	Number of segments with no exposed tree roots present (0-5)
	[3]Root size	Average root diameter of the 5 selected exposed tree roots in each plot
	[4]CWD cover	Estimation of percentage cover of CWD over 10 cm in diameter
	[4]CWD size	Average diameter of the 5 selected CWD in each plot
	[4]CWD decay	Average decay class rating of the 5 selected CWD in each plot, Decay was rated 1-5 based on a modified version of Grove *et al.* (2009)
	[4]CWD empty segments	Number of segments with no CWD substrate available (0-5)
*Temperature (°C)		Average daily temperature calculated over a year
*Relative Humidity (%)		Average daily relative humidity calculated over a year
*Vapour Pressure Deficit (kPa)		Average daily vapour pressure deficit (VPD) calculated over a year

2.3.5. Analysis

Species cover and environmental predictors were analysed at the plot level unless otherwise stated. The average plot-level cover for each bryophyte species was calculated individually for each substrate. This was done by taking a random subset of five quadrats from the plot (quadrats with no bryophytes were included) and averaging the recorded cover for each species from these five quadrats. The combined substrates plot-level species data was calculated by averaging the plot-level data of each individual substrate. In most cases analyses were carried out separately for each age class because many environmental predictors exhibited strong changes with the age of the regeneration forest and thus had strong interaction effects with forest age.

2.3.5.1.Community differences between substrates

PERMANOVA (Anderson, 2001) implemented in Primer PERMANOVA+ was conducted within each age class to determine whether species composition differed among substrates. Plot-level average covers were square-root transformed and a Bray-Curtis similarity matrix was produced. PERMANOVA and follow-up pair-wise comparisons were run with 9999 permutations, with site specified as a random effect factor and substrate type specified as a fixed factor in the design. In addition, a PERMANOVA test was run with all age classes combined to determine if age had a significant impact on bryophyte community composition. For this analysis, forest age and substrate type were included as fixed factors and site was a random factor nested within forest age. PERMDISP (Anderson, 2006), a test for multivariate dispersion, was also conducted in association with each PERMANOVA analysis.

2.3.5.2.Assessing spatial variability within the bryophyte community

Spatial variability within bryophyte communities was also examined using PERMANOVA. For this analysis, the data used was species cover at the quadrat level using only quadrats in which bryophytes were present; this resulted in a maximum of five quadrats per plot for each substrate. Analysis was run separately for each substrate within each age class (i.e. 12 separate analyses). Each PERMANOVA was run with 9999 permutations; quadrat was nested within plot and plot was nested within site. Variability was determined by the estimated variance components output in PERMANOVA. PERMANOVA uses expected mean squares to obtain unbiased estimates of the components of variation in the model in an approach analogous to univariate ANOVA estimation of variance components (Anderson *et*

al., 2008). The quadrat-to-quadrat variability was assumed to be the error term, as quadrat was the lowest level of replication.

2.3.5.3.Bryophyte community maturity level

Bryophyte community maturity was calculated separately for each age class for both the combined species data and for individual substrates. For each combination of forest age and substrate, community maturity was calculated using a one-dimensional canonical analysis of principal coordinates (CAP) (Anderson and Willis, 2003), a constrained ordination approach conducted in Primer PERMANOVA+ V6 software (PRIMER-E ltd, United Kingdom). Plot-level species data was coded as either mature forest or regeneration forest depending on the plot position within transects. A Bray-Curtis similarity matrix was then generated based on the square-root of the plot-level species cover (transformation down-weighted the importance of common species). This matrix then underwent CAP analysis, constrained by mature/regeneration categories. The one-dimensional CAP ordination plot was then orientated so that mature plots were shown to be on the positive (right) side of the CAP1 axis (Fig. 2.2). Maturity of species composition in the regeneration forest plots was determined to be indicated by the higher values on the CAP1 axis (community maturity score); i.e. plots in regeneration forest with species composition closer to the mature forest plots were given a higher maturity score.

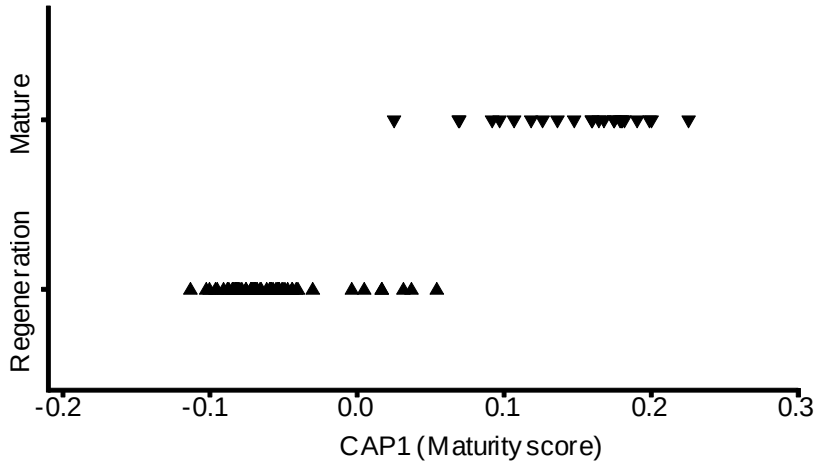

Figure 2.2: One-dimensional canonical analysis of principal components of bryophyte community composition on logs at the ~7 year old sites. This shows and example of the method used to calculate the bryophyte community maturity score. The CAP1 axis represents community maturity with higher values indicating a more mature community composition.

2.3.5.4.Variability in bryophyte community maturity between substrates

Pair-wise differences in plot-level community maturity scores for each of the four different substrates were tested using linear regression in R version 2.15.2 (R development core team, Vienna, Austria). This was done separately for each forest regeneration age class and community maturity data was restricted to plots occurring within the harvested forest.

2.3.5.5.Community maturity predicted by environmental variables

The level of association of individual environmental predictors with bryophyte community maturity scores was also tested using linear regression. Individual environmental factors were tested separately for each combination of substrate type and forest age. Environmental predictors were first transformed to improve the fit of the model using the Box-Cox procedure. For each substrate type, overall plot-level environmental predictors in addition to the substrate-specific predictors (Table 2.1) were tested against community maturity. For the community maturity score for the combined substrates, plot-level environmental predictors plus CWD cover, litter cover, rock cover and bare ground cover were tested. Relationships between the transformed environmental variables and community maturity of the harvested forest plots were analysed using a single factor analysis of co-variance (ANCOVA). In these analyses, site was the first modelled term in order to remove the differences in community composition between study sites. The partial correlation attributed to the environmental variable in the model was attained using the R package `asbio` version 1.0 (Aho, 2013). Microclimate variables were also tested against combined and individual substrate community maturity scores using a single factor ANCOVA, however data was restricted to plots located on the middle transect at each site. All analyses were conducted separately for each age class of regeneration forest.

Model selection, using the Bayesian Information Criterion (BIC) as the selection criterion, was applied to find the set of environmental predictors that best predicted community maturity scores. The set of environmental variables tested in the models were the same as those used in the above analysis. Model selection was done for each substrate and all substrates combined across the three age classes.

2.4. Results

2.4.1. Community differences between substrates and ages

The age of the regeneration forest had a significant impact on bryophyte community composition ($P = 0.007$) as did site ($P < 0.001$). Additionally, substrate type had a significant

effect on composition in all ages of regeneration forest (~7 $P = 0.009$; ~27 $P < 0.001$; ~45 $P < 0.001$), although across all ages classes there was evidence of a significant interaction effect between the substrate and site ($P < 0.001$). Additionally, PERMDISP showed that some substrates had greater variability than others in all age classes (~7 $P = 0.020$, ~27 $P < 0.001$, ~45 $P < 0.001$). Pair-wise testing using PERMANOVA and plotting of substrate communities within each age class using 2-dimensional CAP, provided evidence that the majority of substrates differed in composition from one another across age classes, with the exception of ground - rocks in the ~7 year old forest and roots - rocks in the ~27 year old forest (Table 2.2) (Fig. 2.3).

Table 2.2: Results of the PERMANOVA pair-wise comparisons testing the differences between bryophyte species composition on four substrate types in three regeneration forest age classes. Values listed are P-values generated from 9999 permutations. *not tested due to insufficient numbers of roots available. Significant *P* values are in bold ($P <$ **0.050**); marginally significant values are in italics ($P <$ *0.100*).

Substrate pairs	~7	~27	~45
Ground x CWD	*0.060*	**0.029**	**0.029**
Ground x Rock	0.315	**0.030**	**0.028**
Ground x Root	- *	**0.044**	**0.028**
CWD x Rock	**0.046**	**0.046**	**0.033**
CWD x Root	- *	*0.053*	**0.033**
Root x Rock	- *	0.261	**0.035**

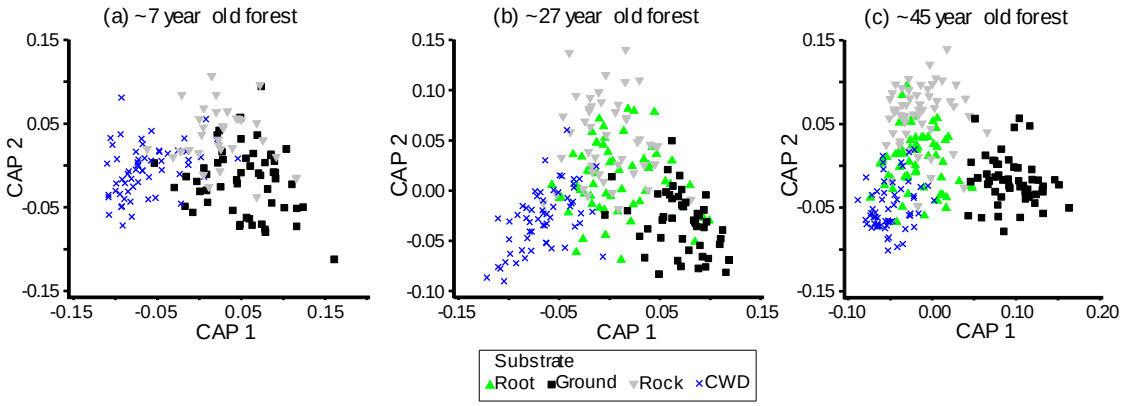

Figure 2.3: Ordination of bryophyte community composition across substrates. Community compositions are plotted using 2-dimensional canonical analysis of principal components, based on a Bray-Curtis matrix. Root substrate is excluded in the ~7 year forest due to lack of occurrence.

2.4.2. Assessing spatial variability within the bryophyte community

Bryophyte community variation was most prominent at the quadrat level. This was consistent across all three ages of regeneration forest, mature forests and across substrates (Fig. 2.4). Within each age class and substrate type, the quadrat level variation accounted for the majority (54.7%) of the total community variability, while the plot level variation (24.3%) accounted for slightly more variability than the site level (20.1%) (Fig. 2.4).

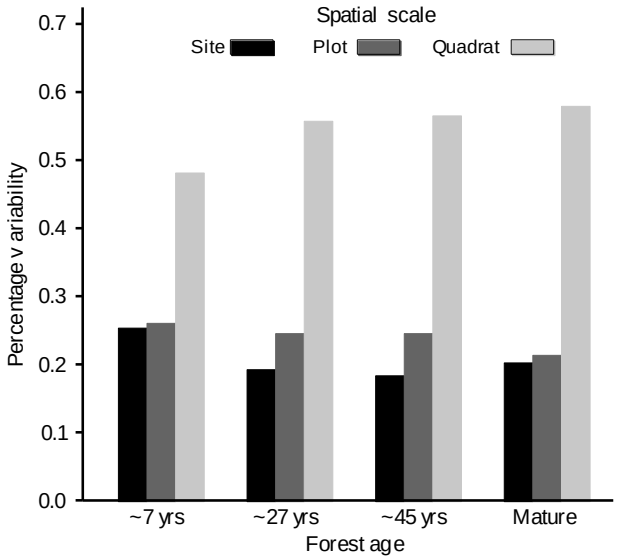

Figure 2.4: Proportion of variability in bryophyte community composition at three spatial scales (site, plot, and quadrat). Variability at each spatial scale is plotted for each of age class examined (~7, ~27 and ~45 years post disturbance and mature forests).

2.4.3. Bryophyte maturity

Variation in the community maturity scores occurred across all ages and for all substrates. The one-dimensional CAP ordination used to predict community maturity showed that forest type (regeneration/mature) was a significant predictor of bryophyte community composition for all ages ($P < 0.001$) and for all substrates within an age class ($P < 0.001$, expect for ~45 ground where $P = 0.035$). However, the ability of the one-dimensional CAP to differentiate between the two forest types decreased with age when all substrates were combined (~7 $R^2 = 0.867$; ~27 $R^2 = 0.703$; ~45 $R^2 = 0.666$), and this trend was consistent across all substrates within an age class.

2.4.4. Variability in bryophyte community maturity between substrates

Plots with more mature communities for one substrate generally also had higher community maturity for the other substrates. Correlations were greatest in the ~7 year old forest, where all substrate combinations were significantly correlated (Table 2.3). The ~45 year old regeneration forest had significant relationships in four out of six substrate pairs and another pair (CWD vs. rocks) was marginally non-significant ($P = 0.094$). The pattern was weakest in ~27 year old regeneration forests, with only two substrates pairs showing significant correlation (Table 2.3).

Table 2.3: Association between bryophyte community maturity for different substrate combinations in three forest regeneration age classes. The correlation (R^2), slope and P-value are reported for each substrate pair in each age class. Significant *P* values are in bold (*P* < **0.050**). Results from the ~7 roots are excluded due to lack of data. Numbers in parentheses are the sample size (n) per test.

Substrate comparison	~7 year old			~27 year old			~45 year old		
	R^2	Slope	P-value	R^2	Slope	P-value	R^2	Slope	P-value
Ground - CWD	0.480 (55)	0.680	**< 0.001**	0.075 (50)	0.042	0.772	0.459 (54)	0.097	0.251
Ground - Rock	0.485 (30)	0.387	**< 0.001**	0.340 (50)	0.170	0.431	0.597 (49)	0.263	**<0.001**
Ground - Root	- (20)	-	**-**	0.216 (50)	-0.026	0.826	0.448 (54)	0.312	**<0.001**
CWD – Rock	0.288 (33)	0.243	**0.026**	0.175 (50)	0.406	**0.041**	0.082 (54)	0.208	0.094
CWD – Root	- (21)	-	-	0.138 (59)	0.179	0.132	0.255 (60)	0.396	**0.002**
Rock – Root	- (10)	-	-	0.143 (50)	0.228	**0.007**	0.242 (54)	0.599	**<0.001**

2.4.5. Environmental variables predicting community maturity

Analysis of the CAP-generated community maturity scores against individual environmental variables showed many of the environmental variables tested were associated with bryophyte community maturity. However, results varied between regeneration age classes and between substrate types (Table 2.4, 2.5). Plot-level maturity was highest near mature forest edges (based on the level of association with the "distance from edge" variable) in both ~27 and ~45 year old regeneration forest, whilst plots with high rock cover and low potential heat load had the greatest maturity in the ~7 year old forest. Additionally, higher leaf area was associated with greater bryophyte community maturity in ~45 year old forests. Community maturity was also highest near the mature forest edge on CWD and rocks across all ages (Table 2.5), as well as on the ground in ~7 year old forest and on roots in the ~45 year old forest. For individual substrates, a combination of plot-level factors, such as leaf area index and potential heat load and individual substrate factors were important in predicting community maturity. On CWD, an increasing decay stage supported a more mature community composition, whilst litter cover and litter depth influenced community maturity

on the ground (Table 2.5). In general there were not many consistent environmental predictors of bryophyte community maturity across substrates or age classes.

Table 2.4: The association between plot level bryophyte community maturity and individual environmental predictors. R^2 values are the partial correlation coefficient of the environmental predictor. Bold numbers indicate *P* value **< 0.050**; +/- shows the nature of the relationship of the environmental variable to maturity level with "+" results meaning that an increase in the environmental variable results in an increase in maturity and "-" results meaning that a decrease in the environmental variable results in an increase in maturity. N = 60 per age class.

	Plot maturity					
Variable	~7		~27		~45	
	R^2	+/-	R^2	+/-	R^2	+/-
LAI	0.008	+	0.036	-	**0.095**	+
CWD cover	0.030	+	0.018	-	0.015	-
Tree diameter	0.014	+	0.218	-	0.005	+
Litter cover	0.000	+	0.005	+	0.010	-
Vegetation cover	0.000	-	0.023	+	0.014	+
Rock cover	**0.071**	+	0.008	-	0.010	-
Bare ground	0.028	+	0.008	-	0.002	-
Heat load	**0.085**	-	0.012	-	0.013	-
Total empty segments	0.029	-	0.006	-	0.003	-
Distance to edge	0.004	-	**0.100**	-	**0.138**	-

Community maturity was also associated with microclimate variables (temperature (°C), relative humidity (%) and (VPD) pressure deficit) but the relationships varied between substrates and age-classes (Table 2.6). Microclimate conditions were most strongly associated with community maturity in the ~45 year old regeneration forest. In this age class, an increase in humidity and a decrease in vapour pressure deficit were predicted to increase community maturity in all four individual substrates (Table 2.6). An increase in humidity also had a significant positive impact on community maturity in the ~7 year old forest for three out of the four substrates (CWD, rocks, ground). Microclimate variables were not good predictors of community maturity in the ~27 year old forest, and the only substrate for which there was a significant level of association was roots, with increasing temperature, VPD and decreasing humidity being associated with more mature communities.

Table 2.5: The association between bryophyte community maturity and individual environmental predictors for each of four substrates (CWD, ground, rocks and roots). R^2 are the partial correlation coefficient of the environmental predictor. Bold numbers indicate *P* value < **0.050**; numbers in italics represent *P* < *0.100*. +/- shows the nature of the relationship of the environmental variable to maturity level with "+" results meaning that an increase in the environmental variable results in an increase in maturity and "-" results meaning that a decrease in the environmental variable results in an increase in maturity. Numbers in parentheses represent the total number of plots that were used in the test.

Variable	CWD maturity						Ground maturity						Rock maturity						Root maturity					
	~7 (60)		**~27** (59)		**~45** (60)		**~7** (55)		**~27** (51)		**~45** (54)		**~7** (33)		**~27** (50)		**~45** (54)		**~7** (20)		**~27** (60)		**~45** (60)	
	R^2	+/-	R^2	+/-	R^2	+/-	R^2	+/-	R^2	+/-	R^2	+/-	R^2	+/-	R^2	+/-	R^2	+/-	R^2	+/-	R^2	+/-	R^2	+/-
LAI	0.002	-	**0.131**	-	**0.091**	+	*0.061*	-	0.044	+	0.015	+	0.007	+	0.085	+	0.027	+	0.049	+	0.038	+	**0.206**	+
Tree diameter	0.012	+	**0.404**	-	0.015	-	0.098	-	0.077	-	0.005	+	0.046	-	0.184	+	0.031	+	0.005	+	0.172	+	0.005	+
Vegetation cover	**0.095**	-	0.027	+	0.040	+	0.001	-	0.001	+	0.006	-	0.004	-	0.035	+	0.001	+	**0.234**	+	0.000	+	0.048	+
Heat load	*0.061*	-	0.004	-	0.014	-	0.021	-	0.034	+	0.004	-	**0.161**	-	0.003	+	0.047	-	0.019	-	0.031	-	0.018	-
Total empty segments	0.036	-	0.001	+	0.015	-	0.002	-	*0.072*	-	0.008	+	0.002	+	0.003	-	0.002	+	0.003	+	0.041	-	0.045	+
Distance to edge	**0.155**	-	*0.051*	-	**0.080**	-	**0.103**	-	0.006	+	0.028	-	*0.097*	-	*0.062*	-	*0.070*	-	0.000	-	0.037	-	**0.166**	-
CWD size	0.006	+	*0.059*	-	0.009	+																		
CWD decay	**0.140**	+	*0.061*	+	0.009	+																		
CWD empty segments	0.001	-	0.021	+	0.009	-																		
CWD cover	0.023	+	**0.090**	-	0.033	-																		
Bare ground							0.017	+	0.029	-	0.014	-												
Litter cover							0.016	-	**0.082**	+	0.014	-												
Litter depth							*0.069*	+	0.002	-	**0.120**	-												
Rock size													0.032	-	0.022	-	**0.091**	-						
Rock cover													0.003	-	0.011	+	0.015	+						
Rock empty segments													0.002	-	0.020	+	0.049	+						
Root size																			0.087	-	0.000	+	0.008	-
Root empty segment																			0.004	-	0.009	-	0.004	-

Table 2.6: Results of linear regressions testing the response of bryophyte community maturity levels to microclimatic conditions. Results are shown at each regeneration age for maturity at the plot level and for the four individual substrates. Maturity was tested against daily average temperature (°C) (Temp), daily average relative humidity (%) (Humidity) and daily average vapour pressure deficit (kPa) (VPD). Bold values represent $P <$ **0.050**, Italic values *P < 0.100*. Numbers in parentheses indicate the number of plots used in each test.

	Temp		**Humidity**		**VPD**	
Substrate	R^2	+/-	R^2	+/-	R^2	+/-
			~7 year old forest			
Plot (19)	*0.177*	+	0.087	+	0.069	-
CWD (19)	0.071	+	*0.173*	+	0.130	-
Rock (13)	0.001	-	**0.570**	+	**0.521**	-
Root (8)	0.004	+	0.137	+	0.140	-
Ground (18)	0.000	+	*0.218*	+	*0.186*	-
			~27 year old forest			
Plot (20)	0.077	+	0.000	-	0.001	+
CWD (20)	0.003	+	0.010	-	0.010	+
Rock (17)	0.015	+	0.000	-	0.000	-
Root (20)	**0.620**	+	**0.234**	-	**0.237**	+
Ground (19)	0.000	+	0.000	-	0.000	-
			~45 year old forest			
Plot (20)	0.073	-	0.123	+	0.126	-
CWD (20)	0.033	-	**0.245**	+	**0.238**	-
Rock (18)	0.109	-	**0.296**	+	**0.308**	-
Root (20)	**0.048**	-	*0.178*	+	*0.186*	-
Ground (16)	**0.459**	-	**0.363**	+	**0.372**	-

When multiple environmental variables were modelled to select the best predictors of bryophyte community maturity, results showed that plot-level conditions such as heat load, leaf area index (LAI) and distance to a mature forest edge were the most consistent predictors across substrates (Table 2.7). Models predicting the community maturity on individual substrates included a combination of plot-level and substrate-specific environmental conditions. This was particularly so for the ground substrate, where litter depth and heat load were consistent predictors, and on rocks where rock size and distance to a mature forest edge were consistent predictors (Table 2.7).

Table 2.7: The top three best models that predict bryophyte community maturity across three forest age classes. Best models are shown for communities at the plot level, and on CWD, ground, rock and root substrates as selected by BIC. Models were predicted separately for each age class of mature forest. Single columns represent terms selected in each model (* indicates the selected environmental variables for the model). R^2 is the correlation coefficient for each model, with bold numbers indicating the model was a significant predictor of community maturity (***P* < 0.050**), italics indicate (*P < 0.100*). See table 2.5 for sample size (n) used in each model selection.

			~7 yr old			~27 yr old			~45 yr old		
		BIC	-5.1	-3.9	-3.9	3.0	4.0	4.2	-1.9	-1.5	1.1
Variable		**R^2**	**0.325**	**0.351**	**0.257**	**0.094**	**0.125**	**0.048**	**0.196**	**0.136**	**0.201**
LAI	**Plot Maturity**		*	*	*				*		*
Heat load			*	*	*		*	*			
Distance to edge						*	*		*	*	*
Vegetation cover											*
Bare ground			*	*							
CWD cover				*							

			~7 yr old			~27 yr old			~45 yr old		
		BIC	-6.7	-5.9	-5.3	-4.0	-3.3	-2.8	2.1	3.0	3.4
Variable		**R^2**	**0.351**	**0.315**	**0.368**	**0.119**	**0.276**	**0.227**	**0.099**	**0.146**	**0.078**
LAI	**CWD Maturity**		*	*	*	*	*	*	*	*	
Heat load			*	*	*						
Distance to edge			*	*	*					*	*
Vegetation cover					*						
Tree diameter				*			*				
Total empty segments											
CWD cover			*								
CWD decay								*			
Litter depth											
Litter cover											

			~7 yr old			~27 yr old			~45 yr old		
		BIC	-2.9	-2.0	-1.7	2.8	3.5	4.4	-10	-9.7	-8.3
Variable		**R^2**	**0.234**	**0.233**	**0.180**	**0.165**	**0.077**	**0.147**	**0.289**	**0.338**	**0.369**
LAI	**Ground Maturity**										*
Heat load			*					*	*	*	*
Distance to edge											
Vegetation cover											
Tree diameter											
Total empty segments						*	*	*			
CWD cover											
CWD decay											
Litter depth			*	*	*					*	*
Litter cover				*		*					

			~7 yr old			~27 yr old			~45 yr old		
		BIC	-1.9	-0.4	-0.1	4.6	5.3	5.9	2.6	2.7	3.2
Variable		**R^2**	**0.261**	**0.374**	**0.301**	0.054	*0.062*	*0.114*	**0.089**	**0.138**	**0.152**
LAI	**Rock Maturity**		*	*	*						
Heat load			*	*	*						
Distance to edge					*		*	*		*	
Vegetation cover											
Tree diameter				*							*
Total empty segments											
Rock size						*		*	*	*	*
Root empty segments											

			~7 yr old			~27 yr old			~45 yr old		
		BIC	4.6	4.8	5.0	-0.1	0.0	0.6	-14	-12	-11
Variable		**R^2**	0.066	0.060	0.049	**0.156**	**0.169**	**0.177**	**0.398**	**0.406**	**0.409**
LAI	**Root Maturity**			*					*	*	*
Heat load						*	*	*	*	*	*
Distance to edge							*		*	*	*
Vegetation cover			*							*	
Tree diameter											
Total empty segments											*
Rock size											
Root empty segments					*			*			

2.5. Discussion

The environmental variation within the regeneration forests studied was sufficient to result in variability in the maturity of bryophyte communities (e.g. Fig. 2.2). Numerous environmental parameters influence bryophyte maturity within harvested forests. By analysing the spatial variability of bryophyte communities we suggest that environmental differences between sites, within the forest and in particular on different substrate pieces all impact bryophyte recolonisation. At the plot level, microclimate, and variables strongly linked with microclimate such as heat load and leaf area index (LAI), were shown to be strongly associated with bryophyte community maturity. However, as well a general forest conditions, specific substrate conditions had a significant impact on the recolonisation of bryophytes communities.

This study demonstrates that recovery of bryophyte communities following timber harvesting is highly variable within sites and between substrates. The quadrat level was the spatial scale at which the majority of variability in bryophyte community maturity was observed (Fig. 2.4). This suggests that the probability of mature bryophyte communities to recover is highly dependent on the environmental conditions of the specific substrate piece. However, the large amount of variability at the quadrat level may also be explained by the stochastic nature of bryophyte recolonisation. Bryophyte colonisation is a highly stochastic process (Fenton and Bergeron, 2013), and due to this, many studies have struggled to model the impact of environmental factors (Pharo and Vitt, 2000; Evans *et al.*, 2012; Fenton and Bergeron, 2013). Modelling against multiple environmental predictors in this study also showed that only a small proportion of variation was explained by environment (Table 2.7). In addition, the high level of variation at the quadrat level may also be an artefact of both substrate size and sampling, which may not have represented the full complement of species present at the plot.

Whilst a large amount of bryophyte community variability at the quadrat level can be explained by stochastic dispersal and sampling intensity, many substrate specific environmental factors were shown to be important in determining the ability for mature bryophyte communities to assemble. For example, factors such as substrate size impacted community maturity. Size often correlates with species richness (Virtanen and Oksanen, 2007) by increasing the amount of micro-environments available (Weibull and Rydin, 2005). For communities on CWD, decay stage was an important predictor of bryophyte maturity in

both ~7 and ~27 year old forests. The importance of decay class is well established (Lõhmus *et al.*, 2007), with higher decay classes supporting higher species richness per log, particularly for mature forest species (Humphrey *et al.*, 2002). However, having a range of CWD decay classes supports a wider range of species at the plot level (Ódor *et al.*, 2006). Traditional forestry methods result in a pulse of CWD of the same decay class, whereas natural disturbance provides an ongoing supply of CWD from death and collapse of trees, and thus a greater variety of decay classes at any one point in time (Grove *et al.*, 2009). Having CWD in the later stages of decay was shown to be important in developing mature forest communities, especially in the younger regeneration forests which tended to have the majority of CWD in early decay stages.

Although spatial variability analysis showed the majority of variability in bryophyte community composition occurred at the quadrat level, within plots, community maturity was highly correlated between substrates. Additionally results confirmed that within-site variability in bryophyte community maturity was associated with plot level differences in environmental parameters, particularly microclimate. This suggests that plot level environmental factors are likely to be important influences on community maturity regardless of substrates.

Of the plot level environmental factors; heat load, distance to a mature forest edge and leaf area index were strong environmental predictors of bryophyte community maturity. Leaf area index (canopy cover) has strong impacts on bryophytes (Coote *et al.*, 2013), and maintaining greater canopy cover during harvesting (e.g. with dispersed retention) leads to higher bryophyte retention (Halpern *et al.*, 2012; Caners *et al.*, 2013a). Potential heat load describes the amount of radiation that would be received in the absence of canopy, and is calculated using both slope and aspect. These two factors are known to mediate the response of bryophyte communities to clear cut logging (Åström *et al.*, 2007). In a study of vascular plant succession at the sites studied for this project, Balmer et al. (in preparation) also demonstrated the importance of slope and aspect on the recovery of vascular plant. Potential heat load and LAI also have a strong impact on ground-level microclimate conditions, as has been shown in a previous study based at these sites (Baker *et al.*, 2014). Microclimate is a well known driver of bryophyte community composition (Stewart and Mallik, 2006; Ódor *et al.*, 2013; Halpern *et al.*, 2014). Microclimate conditions predicted bryophyte community maturity across multiple substrates, particularly in the oldest forest age. Furthermore, microclimate conditions generally explained more variation in bryophyte community

maturity than the other environmental predictors. This confirms that it is one of the most important factors in the recolonisation of bryophytes.

Distance to a forest edge was also a predictor of bryophyte community maturity. Mature forest proximity is known to influence microclimate conditions within disturbed forests due to mechanisms such as shading and air flow from standing forests (Baker *et al.*, 2014; Dovčiak and Brown, 2014). The effect of distance from the mature forest edge on micro-climate at the sites of the present study sites has been documented (Baker et al. 2014). However, reduced distances to the mature forest edge can also aid bryophyte recolonisation by providing closer sources propagules (Baker *et al.*, 2013a), which would be beneficial to dispersal-limited bryophytes. Reduced dispersal distance will also increase the total availability of spores near to mature edges due to strong leptokurtic spore distribution patterns (Söderström and Herben, 1997), meaning that even well dispersed species would have a greater chance of recolonisation near an edge. The finding in the present study that reduced distance to mature forest edge was associated with increased bryophyte community maturity is likely to be due to a combination of better dispersal and buffered microclimate (Caruso *et al.*, 2011; Baker *et al.*, 2013b). However, due to the similar responses in the change of microclimate conditions and dispersal ability with distance to a forest edge, results here cannot partition the importance of each factor. It is most likely that both dispersal distance and variation in microclimate play an important role in the recolonisation of bryophyte communities.

In this study it was established that 20% of the observed community variation occurred between sites. This variation is likely to be due to macro-environmental differences between sites such as macro-level temperature, rainfall variation (Berg *et al.*, 2002), fire history and stochastic variability in the distribution of source populations of individual bryophyte species. For the same study sites, Balmer et al. (in preparation) determined that variation in rainfall and fire histories were associated with differences in floral communities. Similarly, differences in macro-landscape factors may contribute to site-to-site variation in bryophyte community composition, including the abundance of mature forests in surrounding landscapes (Wardlaw *et al.*, 2012). Factors such as these are important considerations for regional landscape management.

This study showed environmental conditions across multiple scales impacted on bryophyte maturity regardless of age of the forest. However, there was strong variation in the

specific environmental predictors that were important for each age class. Temporal responses to environmental conditions are important to consider, as recolonisation is likely to occur over extended time periods. Whilst our study did not show many consistent trends between the forest age classes, microclimate conditions were a strong and consistent predictor of bryophyte community maturity in the 45 year old forest; this may be in response to the increased time to recolonise and establish community distribution patterns in response to the environmental drivers. The absence of expected patterns in the 27 year old regeneration forest requires further study to determine if it was simply an anomalous result, or whether successional processes in this forest age class differ due to specific mechanisms and processes associated with forest succession. Corresponding to the observed anomalies in the bryophyte community in the 27 year old forests, Balmer et al. (in preparation) found that vascular plant species richness was lowest in this age class, attributed in part to increased competition at the ground layer from the sedge *Gahnia grandis* and increased shade due to canopy closure.

2.5.1. Conclusions and implications for forest management

Recolonisation of mature bryophyte communities in harvested forests is driven by many environmental variables; some were substrate-specific factors and others were indicative of general plot-level conditions. Testing of environmental predictors showed condition more similar to mature forest supported a more mature bryophyte flora. Previous studies have demonstrated that the retention of mature forest elements within harvested forest is associated with higher bryophyte richness (Pharo and Lindenmayer, 2009; Caners *et al.*, 2013a; Hofmeister *et al.*, 2015). In addition, increased retention of mature forest elements has been shown to improve the recovery in a variety of other taxa (see Kuuluvainen and Grenfell (2012) or Fedrowitz *et al.* (2014) for review). Harvesting practices designed to encourage "mature" environmental conditions within harvested forests can promote a more rapid return of pre-disturbance communities (Seidl *et al.*, 2014) and in general make the ecosystem more resilient to impacts from disturbance (Drever *et al.*, 2006). For example, this study highlighted that microclimate is a key element in creating bryophyte maturity. Microclimate can be adjusted by variable retention harvesting approaches such as dispersed or aggregated retention via "forest influence" (Heithecker and Halpern, 2006; Baker *et al.*, 2014; Dovčiak and Brown, 2014).

Within a plot, bryophyte community maturity levels tended to the same, independent of substrate type. This suggests that forestry techniques, such as retention forestry, that create

mature environments within the harvested forest will be beneficial for a variety of bryophyte communities. However, observed differences in communities between substrates and the importance of substrate-specific environmental factors shows that individual substrate communities may need to be considered separately as part of forest management. Previous studies have shown that recovery rates of communities following disturbance differs between substrates (Dynesius, 2015) and maintaining substrate diversity benefits cryptogram conservation (Lõhmus *et al.*, 2007). Therefore, individual substrates need to be considered in forest management (Takala *et al.*, 2014) e.g. longer rotation creating larger logs and roots or reducing burial of rocks during mechanical disturbance.

Finally, this study showed that the importance of environmental variables in predicting bryophyte maturity changes with time since disturbance. This may be partly due to the stochastic nature of bryophyte recolonisation (Fenton and Bergeron, 2013), but also may be due to the changes in species life history characteristics with bryophyte succession or changing environmental conditions with forest succession. For example, biological traits associated with early seral species enable their survival and growth in post harvested conditions, whereas traits of closed canopy species can be particularly sensitive to changes in light and microclimate (Caners *et al.*, 2013b). Temporal trends are therefore important to consider when monitoring the benefits of management techniques, as creating conditions which support recolonisation of early seral species may not aid the recolonisation of late seral species.

Chapter 3.
The effects of forest influence on microclimate

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(see Appendix 3)

3.1. Abstract

A major aim of sustainable forest management is the maintenance or recolonisation of harvested areas by species that were present pre-disturbance. Forest influence (a type of edge effect that focuses on the effect of mature forests on adjacent disturbed forest) is considered to be an important factor that contributes to the success of mature forest species recolonising disturbed areas. Forest influence occurs in two main ways by: 1) by providing a source of propagules or individuals for recolonisation; and 2) by its influence on the biotic and abiotic conditions of the disturbed forest. This study focuses on forest influence's impact on microclimate conditions of adjacent disturbed areas regenerating after harvesting. In particular, the study investigates whether microclimate within a regenerating forest changes with increasing distance from a mature forest edge, and whether the magnitude of microclimatic change varies over diurnal, seasonal and successional time scales.

Results of the study showed that the microclimate of regenerating forests is affected by the distance to a standing mature forest. Temperature, relative humidity, vapour pressure deficit, and the short-term fluctuations of these microclimate parameters were influenced by nearby mature forest. In addition, the study found that the magnitude of forest influence changes over diurnal, seasonal and successional time scales. For example, it was discovered that forest influence is greatest during the middle of the day, during the summer months when solar heating is greatest and on hot windy days. Critically, the impact of forest influence peaked around ~27 years after disturbance in the areas studied, with less influence shortly after disturbance. We speculate this is due to lower levels of midday shading in the ~7 year old forest. Forest influence of microclimate persisted in regeneration areas that were harvested 45 years ago, although the magnitude and importance of the effect was low.

We conclude that proximity to mature forest stands (forests influence) impacts the microclimate of forests regenerating after disturbance, although the response is quite variable through time. Our results provide insight into the role of microclimate on the success of mature forest species to successfully recolonise after disturbance. Management practices, such as aggregated retention and other forms of retention forestry, which increase the proportion of harvested area under forest influence, may provide a mechanism to promote the recolonisation of mature-forest species.

3.2. Introduction

Sustainable forest management is increasingly focused on facilitating the survival and/or re-establishment of biodiversity in forests regenerating after disturbance (Franklin *et al.*, 1997; Lindenmayer *et al.*, 2012). Within disturbed landscapes, edges between disturbed and mature forest patches become prominent ecological features. These edges allow the flow of energy, nutrients and species from one forest type to another (Murcia, 1995; Strayer *et al.*, 2003; Hufkens *et al.*, 2009). While almost all previous studies of edge effects have focused on the impact of disturbed forests on adjacent mature forest (e.g. Harper *et al* (2005)), it has recently become clear that the inverse edge effect (the impact of mature forest on adjacent disturbed forest or "forest influence") affects the recolonisation of disturbed areas by mature-forest species. Forest influence includes biological processes, such as the distance that species can disperse from mature forest, as well as physical characteristics, such as how microclimate changes with distance from mature forest (Mitchell and Beese, 2002; Beese *et al.*, 2003). Forest influence is characterised both by magnitude – how different the edge-influenced zone is from a non-edge influenced zone (Harper *et al.*, 2005), and geographic scale – the distance from an edge up to the most interior area in which conditions are still significantly different from unaffected interior conditions (depth of edge influence) (Chen *et al.*, 1992; Harper and Macdonald, 2001).

As mature and regenerating forests differ markedly in microclimate, it is reasonable to expect gradients rather than abrupt changes in microclimate across the boundary between these forests. Such gradients are well studied in traditionally examined edge effects into undisturbed forest (Matlack, 1993; Chen *et al.*, 1995; Gehlhausen *et al.*, 2000), but only a few studies have examined the inverse edge effects of "forest influence" on microclimate, these studies occur in either forests next to permanent/newly deforested areas (Cadenasso *et al.*, 1997; Davies-Colley *et al.*, 2000; Huggard and Vyse, 2002), and 4-7 year old regenerating forest (Redding *et al.*, 2003; Heithecker and Halpern, 2007). Related studies have shown that temperature (both soil and air), humidity, light levels and wind speed of disturbed forest all change with distance from a stream (Anderson *et al.*, 2007; Rykken *et al.*, 2007), although streams would be expected to create different microclimatic conditions than anthropogenically created edges. Microclimate gradients are important to understand because change impacts many forest organisms – such as beetles (Grimbacher *et al.*, 2006) and bryophytes (Proctor, 1990; Stewart and Mallik, 2006) – and functional processes within ecosystems, including nutrient and water cycles (Chen *et al.*, 1995; Riutta *et al.*, 2012).

Several studies have proposed that microclimatic effects can contribute significantly to forest influence on species re-establishment in disturbed areas (Hansen *et al.*, 1993; Tabor *et al.*, 2007; Baker *et al.*, 2013b; Fountain-Jones *et al.*, 2015).

A major driver of microclimate in the understorey of a forest is the amount of light that reaches an area (Matlack, 1993). Although the density of the immediate overhead canopy is the strongest determinant of the quantity of light (Matlack, 1993; Davies-Colley *et al.*, 2000), shading from more distant mature trees in nearby undisturbed forest also can reduce understorey irradiation levels in disturbed areas (Young and Mitchell, 1994; Cadenasso *et al.*, 2003; Godefroid *et al.*, 2006), and therefore create forest influence. Microclimatic forest influence can extend past the point where shading from a mature forest is significant (Godefroid *et al.*, 2006), potentially through the flow of cold, moist air into the regeneration forest.

The small amount of literature on microclimatic forest influence all focuses on single aged forests, generally in the years immediately after disturbance. However, changes in the magnitude and geographic scale of microclimatic forest influence on long, medium and short time scales should be expected because similar effects have been observed in studies of interior edge effects (Mesquita *et al.*, 1999; Denyer *et al.*, 2006). However this concept has only been examined once previously for forest influence (Dovčiak and Brown, 2014), in American hardwood forests. Increases in canopy cover as disturbed forests age are likely to cause decreases in the magnitude of forest influence as the microclimate of the regeneration forest ultimately returns to pre-disturbance conditions (Halpern and Lutz, 2013). As well as changes with forest age, the magnitude and distance of forest influence is expected to change over shorter time scales. For example, edge effects into mature forest vary with precipitation (Harper *et al.*, 2005), solar irradiation (Miller, 1980; Davies-Colley *et al.*, 2000; Xu *et al.*, 2002), wind speed (Chen *et al.*, 1995; Davies-Colley *et al.*, 2000), time of day (Saunders *et al.*, 1999; Denyer *et al.*, 2006) and season (Young and Mitchell, 1994; Silbernagel *et al.*, 2001; Wright *et al.*, 2010). Periodic changes in the magnitude of microclimatic forest influence could result in unique species responses depending on the phenology of the species. For example, beetle communities showed strong seasonal patterns in Tasmanian wet forests (Grove and Forster, 2011) and the germination and shoot elongation of Australian rainforest plants was affected by growing season temperature (Read, 1989).

This study will focus on the poorly investigated question of how forest influence changes over time. This information will facilitate forest management planning that aims to enhance species persistence in disturbed landscapes. Knowledge of the duration, and short-term temporal shifts, in forest influence could be combined with knowledge of the landscape and species' life histories to better predict the outcomes of management. We use evidence from transects running from mature forests into three age classes of regenerating forest. Based on previous studies of microclimate in disturbed forests and the impact that edge effects has on microclimate in mature forests, we hypothesised that:

(1) Mature forests have more stable microclimates than regenerating forests;

(2) The differences in microclimate between mature forest and regenerating forest diminish as regenerating forests develop (i.e. there is microclimatic succession);

(3) The microclimate of regenerating forest near an edge with mature forest will more similar to mature forest conditions than microclimate of the interior of the regenerating forest (i.e., there is microclimatic forest influence);

(4) The magnitude of forest influence will change with time on short (diurnal), medium (seasonal) and long (successional) time scales; and

(5) Forest influence on microclimate will vary with background conditions of rainfall, wind, and temperature.

3.3. Methods

3.3.1. Study sites

We studied 15 sites in the southern production forests of Tasmania, Australia (Fig. 3.1A). Each site contained mature forest adjacent to forest regenerating after clearfell burn and sow (CBS) timber harvesting. This silviculture involved removal of all major trees and piling of all other vegetation followed by a regeneration burn and aerial sowing of eucalypt seed. Apart from substantial quantities of coarse woody debris habitat and rare individual trees left in some sites, CBS harvesting effectively removes the majority of flora and fauna, requiring re-establishment post-disturbance. The mature forest contained emergent trees of *Eucalyptus obliqua* and/or *Eucalyptus regnans* averaging >30m tall, over a closed canopy of rainforest trees (*Nothofagus cunninghamii* and/or *Atherosperma moschatum* with other species such as *Eucryphia lucida*, *Phyllocladus aspleniifolius* and *Anodopetalum biglandulosum*).

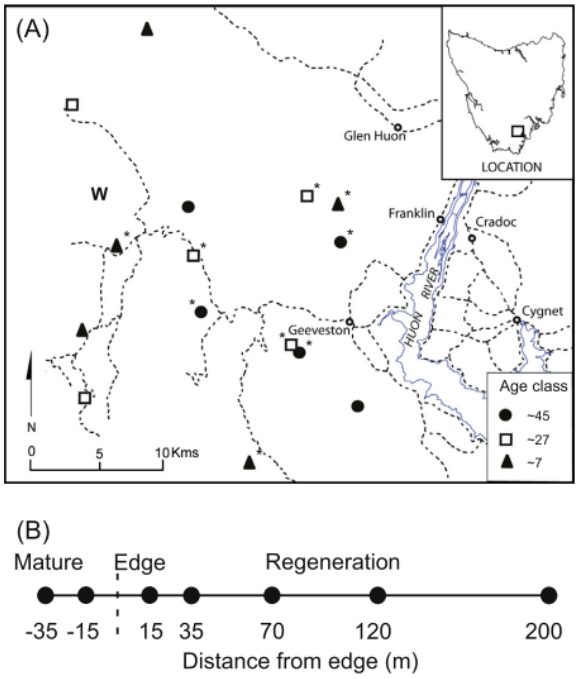

Figure 3.1: (A) The location and age class of the 15 study sites in Tasmania, Australia (* indicate sites that were used in both summer and winter collection periods). **W** indicates the location of the Warra Bureau of Meteorology weather station. (B) Layout of plot locations on transect at each site in relation to the edge of the mature and regeneration forest, "-"distance refer to a plot within the mature forest.

3.3.2. Experimental design

Five sites in each of three age classes of regeneration forests were selected: "~7 year old" forest, harvested between 2002 and 2007; "~27 year old" forests, harvested between 1983 and 1989; and "~47 year old" forests, harvested between 1966 and 1972 (plate 1). The CBS harvesting was relatively consistent across all age classes apart from slightly higher levels of coarse woody debris in older sites. The ~7 year old regenerating forest typically had a sparse canopy of eucalypt trees on average 7 m tall; the ~27 year old forest typically had reached canopy closure, with a canopy ~22 m tall; and the ~47 year old forest had closed canopy ~27 m tall. The mature forest was not significantly damaged by wind or fire during or after the timber harvest activities. All sites were chosen to minimise systematic differences in environment and topography across sites and so that the forest prior to clearfelling was likely to have been similar to the retained mature forest.

Within each site, seven study plots were established along a single transect running perpendicular to the mature/regeneration boundary (Fig. 3.1B). Each transect comprised two

data collection plots within the mature forest (-35 m and -15 m from the edge) and five plots in the regeneration forest (15 m, 35 m, 70 m, 120 m and 200 m from the edge).

3.3.3. Observations

At each plot, a HOBO U23 pro V2 temperature/humidity data logger (ONSET, Massachusetts) was deployed to record the temperature and relative humidity every 30 minutes. Each data logger was mounted on a steel post such that the detector was 50 cm above the ground and housed in a solar protection shield to avoid direct solar radiation; sensors were calibrated before deployment by running loggers simultaneously in set environmental conditions. Two periods of recording were conducted: 1) all loggers were deployed for 142 days in summer and autumn (December-May 2011-2012); and 2) the loggers at -35 m, 15 m, 35 m and 200 m plots were deployed in three out of the five sites per age class (9 sites, Fig 3.1) for an additional 213 days spanning winter and spring (May-December 2012). Due to deployment, collection and translocation, data was only partially collected for the months of December 2011, May 2012 and December 2012.

Temperature and relative humidity were used to calculate vapour pressure deficit (VPD) (Allen *et al.*, 2005) (Table 3.1). VPD describes the drying capacity of the air with increased evaporation rates at high VPD. Leaf area index (LAI) was estimated for each plot from digital hemispherical photographs using Gap Light Analyzer (Cary Institute of Ecosystem Studies, New York, USA). LAI describes the density of the plant canopy. Temperature at 3 pm, average wind speed (generated as the average of the 9am and 3pm wind speeds and the maximum daily wind gust) and two-day rainfall (total of the current and previous day's rainfall), were calculated from automatic weather station data, located at Warra (Tasmanian Bureau of Meteorology Station no. 097024) (Fig. 3.1A).

3.3.4. Statistical analysis

Data were initially screened and obvious errors, indicated by large spikes in microclimate variables, were replaced by missing values, the remaining data was examined to ensure it followed typical daily patterns. The 30 minute observations were averaged into a variety of variables (Table 3.1). In situations where hourly average data were used, averages were first calculated per hour of each day then averaged across the study period for an overall average for each hour. Short-term fluctuation in microclimate metrics were obtained for each 30 minute measurement by calculating the absolute change from the previous 30 minute value. Differences between the 200 m and 15 m plots in the regeneration forest (Δ200m-15m)

were calculated using the both the daily and monthly average values at the plot level. Data analysis was confined to the summer–autumn collection period, unless specified, as there was a higher level of replication compared to the winter–spring period. All analyses were conducted in R version 2.15.2 (The R foundation for Statistical Computing, 2012).

Table 3.1: Microclimate variables used in the study of forest influence in Tasmania, Australia and the rationale and calculation method for each variable. Each variable was calculated separately for temperature (°C), relative humidity (%) and vapour pressure deficit (kPa) for each plot.

Variable	Calculation method.	Rationale
Afternoon average	Average of all observations from 1300 to 1600 hrs. Average was calculated for the regeneration (120 and 200 m plots) and mature forest (-15 and -35 m plots). Average was calculated per site.	Hottest and least humid period of the day, microclimate driven by sun and shading.
Night average	Average of all observations from 0400 to 0700 hrs. Average was calculated across two regeneration (120 and 200 m) plots per site and across two mature forest (-15 and -35 m) plots per site.	Coldest and most humid period of the day, microclimate driven by canopy cover trapping reflected radiation and moisture.
Short-term fluctuation	Average of the change in observation from the previous 30 min recording. All recordings were used to get an average for the regeneration (120 and 200 m plots) and mature forest (-15 and -35 m plots) separately per site.	Determines the stability of microclimate. Stable forests have low short-term fluctuations; mature forest species are generally adapted for stability.
Average Hourly Δ200m-15m	The difference between the averaged hourly observation at the 200 m and 15 m plots. Hourly averages were calculated per plot from the data across the summer period.	Indicator of the magnitude of forest influence. Used to determine diurnal changes.
Daily average Δ200m-15m	The difference in the average daily observation between the 200 and 15m plots. Data was averaged per plot per day, then across all days to get a single site value. Site values were then averaged to get an age class value.	Indicator of the magnitude of forest influence. Used to determine daily changes.
Monthly average Δ200m-15m	The difference between the averaged monthly observation at 200 m and 15 m plot. Monthly averages were calculated for these plots from all observations per month. Contains data from both summer and winter collection periods.	Indicator of the magnitude of forest influence. Used to determine yearly changes.

3.3.4.1.Microclimatic succession

Changes in microclimate (short-term fluctuation, afternoon and night metrics for temperature, relative humidity and VPD) and leaf area index (LAI) with forest age were

analysed based on the average values for -15 and -35 m plots (mature forest) and the average of values for 120 and 200 m plots (representing the regenerating forest). Whether mature forest differed from each age class of regenerating forest was tested using ANOVA, with contrasts set to test each regeneration age class against its associated mature forest, ANOVAs were run separately for each metric. Whether the three age classes of regeneration forest were different was tested using one-way ANOVAs.

3.3.4.2.Drivers of microclimate in harvested forests

To explore the factors which influenced microclimate conditions in regeneration forests, we used multiple linear regression with the continuous predictors of LAI; distance to a mature forest edge; "northness" - the direction towards the mature forest edge (see below); and an index of potential heat load calculated from plot aspect, slope and latitude (McCune and Keon, 2002). The potential heat load In(Rad, MJ $\cdot cm^{-2} \cdot yr^{-1}$) estimates the irradiance that would be received under full sunlight (i.e. no canopy or clouds). Northness measurements were calculated as the cosine of the angle of the direction of the edge (Pierce *et al.*, 2005), which converts the edge direction to a linear variable. Age class of the regeneration forest was a categorical predictor. Predictor variables were examined for collinearity before model testing. Every combination of the continuous predictors, including interactions with age class, was tested against afternoon microclimate metrics to identify the model which best predicted afternoon microclimate variables. Models were compared for data divided into individual age classes (16 models per age class) in order to determine if important factors varied with the age class of the regeneration forest. No interaction terms were examined for multiple linear regression models in the individual age classes, as this method was used to examine the most important individual predictors.

The best models were selected using the Bayesian Information Criterion (BIC). This metric was used in preference to Akaike's information criterion, which is more prone to over-fitting than BIC (Rawlings *et al.*, 1998), and we wished to identify the most important factors that determine microclimate. Models were selected for further examination if the difference in BIC between that model and the best model was less than two BIC units. Once model selection was completed, the importance of the factors was additionally assessed using the P-values of the coefficients in the linear models selected. Relative importance was also assessed using the LMG technique (Lindeman *et al.*, 1980) implemented in the R package `relaimpo` v2.2 (Gröemping, 2006). LMG estimates the percentage of the variance each term in the

model explains by averaging the sequential sum of squares for all possible orders of terms (Lindeman *et al.*, 1980).

3.3.4.3.Changes in forest influence on short and medium time scales.

Changes in forest influence over short (diurnal) to medium (monthly) temporal scales were assessed using a metric of the magnitude of forest influence (Δ200m-15m: the difference between the 200 m and 15 m plots for a given parameter). The 200 m and 15 m regeneration plots were selected as it was assumed that the 15m plot would be the most heavily influenced and the 200m plot would be the least influenced by the mature forest.

Diurnal changes in the magnitude of forest influence in terms of a selected range of microclimate variables were assessed graphically by plotting the hourly mean of Δ200m-15m for each of the three age classes. Monthly changes in forest influence were assessed by plotting the monthly mean of Δ200m-15m for each of the age classes. Due to temporal autocorrelation, we did not conduct statistical tests, but instead used graphical examination. The winter data set was also included in the analysis of monthly change. Data from May were not included as data loggers were translocated during this period.

3.3.4.4.Changes in forest influence with background environmental conditions

The impact of macroclimate on forest influence was determined by correlation analysis of the daily average Δ200m-15m against three daily climate measurements; 3pm temperature, average wind speed, and two-day rainfall at the nearby Warra automatic weather station. Separate correlations were estimated for each age class and each of the three microclimate variables; temperature, relative humidity and VPD. Individual significance values for these analysis were adjusted separately within each age class, using the Holm-Bonferroni method (Holm, 1979). Multiple linear regressions were used to determine the impact that combinations of background environmental variables had on the daily average Δ200m-15m.

3.4. Results

Patterns in LAI indicated key structural differences between forest age classes. The ~7 year old regeneration forest had the lowest mean LAI (1.67 ± 0.40 SE), with higher values in ~27 year old (2.28 ± 0.35 SE) and ~45 year old (2.61 ± 0.61 SE) forests. LAI was lower in all three ages of regeneration forest than in mature forest, although these differences were significant for ~7 ($P = 0.049$) and ~45 ($P = 0.037$), but not ~27 ($P = 0.110$) year age classes. LAI in mature forest increased with the increase in age of the adjacent regeneration forest, the

lowest levels of LAI in mature forests occurred when adjacent to ~7 year old regeneration forest (2.34 ± 0.77 SE). Levels increased when next to ~27 year old regeneration forest (2.82 ± 0.47 SE) and LAI was highest in mature forests adjacent to ~45 year old regeneration forest (3.32 ± 0.30 SE).

3.4.1. Microclimatic succession

In accordance with hypotheses 1 and 2, areas of mature forest had more stable microclimates than regeneration forest, and the differences in microclimate between mature and regeneration forests decreased with increasing age of the regeneration forest.

Increased stability in mature forests was highlighted by smaller short-term fluctuations in temperature ($P = 0.003$), humidity ($P = 0.028$), and VPD ($P = 0.012$) compared to the ~7 year old regeneration forest. Mature forests also tended to have smaller short-term fluctuations in microclimate variables compared to ~27 and ~45 year old forests, however these differences were non-significant ($P > 0.150$) (Fig. 3.2D, E, F). Regeneration forests had higher afternoon temperature and VPD and lower levels of relative humidity in all three age classes of regeneration forest compared to the associated mature forests (Fig. 3.2A, B, C).

The ~7 year old regeneration forest generally had the greatest differences in microclimate with mature forest; this was true for all afternoon and daily short-term fluctuation variables. In general, the scale of the differences between mature and regeneration forests diminished with the age class of the regeneration forests, although the ~27 and the ~45 year old regeneration forests were not significantly different in any of the metrics ($P > 0.05$). Compared to the ~27 and ~45 year old regeneration forests respectively, the ~7 year old regeneration forest had higher average afternoon temperature ($P = 0.053, 0.011$) and VPD ($P = 0.070, 0.028$), lower afternoon relative humidity ($P = 0.093, 0.041$), and greater short-term fluctuation of temperature ($P = 0.031, 0.012$), relative humidity ($P = 0.053, 0.041$) and VPD ($P = 0.048, 0.028$) (Fig. 3.2)

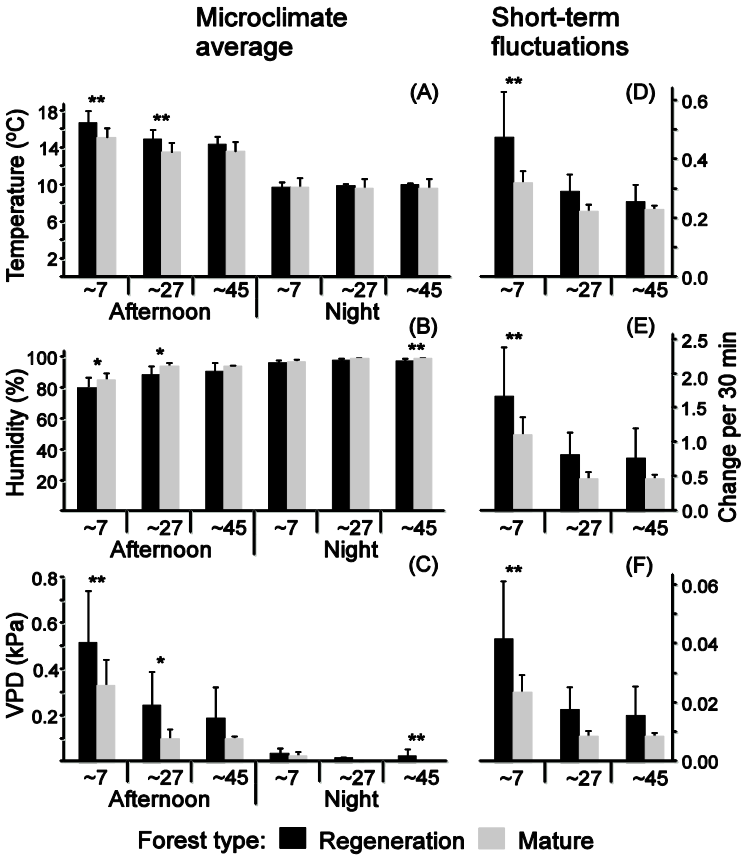

Figure 3.2: Variation in microclimate according to forest type (mature vs. regeneration) and age class, in Tasmania, Australia. Average afternoon and night time temperature for forest type and age class (A). Average afternoon and night relative humidity with change in forest type and forest age class (B). Average afternoon and night vapour pressure deficit (VPD) with changes in forest type and age class (C). Short-term fluctuation of temperature (D), short-term fluctuation of relative humidity (E), and short-term fluctuation of VPD (F). Short term fluctuation was measured as the average change from one 30 min recording to the next. ** indicates the mature forest was significantly different to the regeneration forest ($P < 0.050$), * indicates marginal significance ($P < 0.100$).

For the night period, there were no differences between regeneration and mature forests within an age class or across age classes of regeneration forest ($P > 0.130$) except in the ~45 year old forest sites where humidity was lower in the regeneration forest ($P = 0.031$) and VPD was higher ($P = 0.033$) (Fig. 3.2).

The mature forest microclimate was affected by the age of the associated disturbed forest, with mature forests plots adjacent to the ~7 year old regeneration forests experiencing higher temperatures, VPD and short-term fluctuations as well as lower relative humidity compared to mature forest adjacent to the older regeneration age classes (Fig. 3.2).

3.4.2. Drivers of microclimate in harvested forests

Exploratory analyses to examine the best model for predicting afternoon microclimate variables suggested that age class interacted with numerous factors and was a key factor in predicting the best models. However, analysis of each age class separately informed which factors were best at predicting afternoon microclimate variables (Table 3.2). In most cases, the BIC-ranked model selection, linear model factor significance, and LMG relative importance analysis provided consistent supporting evidence about which factors were most important in predicting the afternoon microclimate variables.

Distance to mature forest edge only affected microclimate in the ~27 year old regeneration forests, with microclimate in the other age classes responding to other factors. LAI was the only predictor in the best model for temperature and VPD in the ~7 year old regeneration forest; and the best model for humidity had LAI and edge direction as factors, with LAI having the greatest importance (Table 3.2). Alternative models (i.e., those with a BIC within 2 of the best model) included other factors, but LAI was always the most important. When included in additional multiple regression models, distance was always a non-significant effect for this age class. In the best models for ~27 year old regeneration forest, LAI was highly significant and the most important factor, although distance also had a highly significant effect for all three microclimate parameters (Table 3.2). By contrast, potential heat load was the most important factor present in the best models for the ~45 year old regeneration forest for all three microclimate parameters. The direction to a mature forest edge was also an important in predictor in ~45 year old forests. Distance was included in additional multiple regression models predicting both humidity and VPD, however was always non-significant (Table 3.2).

Table 3.2: The most parsimonious linear models predicting afternoon microclimate variables. Models were run for each variable (temperature, humidity, and vapour pressure deficit (VPD) per age class of forest regenerating following clearcutting. Linear models were used to see which terms best predicted the given microclimate variable and only models in which the Bayesian information criterion (BIC) was within 2 of the best model are shown. For each model, the relative importance metric (LMG) which expresses the proportion of model variation explained by the individual factor is shown for each effect in the model (a dash indicates that this factor was not in the model). Bold-highlighted numbers indicate that the factor had a significant impact on the afternoon microclimate variable ($P < 0.050$) in the linear model; underlined numbers indicate the factor had a marginally significant impact ($P < 0.10$). Model factors are; LAI (leaf area index), edge dir. (northness; direction of the mature forest edge), heat load (ln(Rad, $MJ.cm^{-2}.yr^{-1}$)) (measure of site slope, aspect and latitude) and distance (plot distance from a mature forest edge (metres)).

Average afternoon temperature Model terms					**Average afternoon humidity Model terms**					**Average afternoon VPD Model terms**				
BIC	*LAI*	*Edge dir.*	*Heat load*	*Distance*	**BIC**	*LAI*	*Edge dir.*	*Heat load*	*Distance*	**BIC**	*LAI*	*Edge dir.*	*Heat load*	*Distance*
~7 year old regeneration forest														
74.54	**1.000**	-	-	-	170.80	**0.776**	0.224	-	-	-0.95	**1.000**	-	-	-
76.13	**0.869**	-	0.131	-	171.01	**1.000**	-	-	-	0.16	**0.884**	0.116		-
					172.28	**0.745**	0.202	-	0.053	0.78	**0.943**	-	-	0.057
~27 year old regeneration forest														
62.82	**0.532**	0.067	**0.162**	**0.239**	158.94	**0.516**		0.123	**0.359**	-23.29	**0.535**	-	0.122	**0.343**
63.78	**0.535**	**-**	**0.207**	**0.258**	159.32	**0.652**	-	-	**0.348**	-23.29	**0.670**	-	-	**0.330**
~45 year old regeneration forest														
64.51	-	**0.307**	**0.693**	-	147.23	-	-	**1.000**	-	-39.42	-	-	**1.000**	-
					148.53	-	-	**0.933**	0.067	-38.08	0.044	-	**0.956**	-
					148.73	0.038	-	**0.962**	-	-37.87	-	-	**0.938**	0.062
					149.17	-	0.159	**0.845**	-	-37.70	-	0.150	**0.850**	-

3.4.3. Changes in forest influence on short and medium time scales

The magnitude of microclimatic forest influence (Δ200m-15m), showed a clear diurnal pattern for all of the studied age classes and each of the studied metrics (average hourly temperature, relative humidity and VPD). Thus Δ200m-15m increased in magnitude (i.e., diverged further away from zero), from early morning (0800 hrs) until the mid-afternoon (1500 hrs), then decreased until approximately 2200 hrs (evening), and stayed steady overnight. This trend was very prominent in the ~27 year old forest and to a smaller degree in the ~45 year old forest for all three studied metrics (Fig. 3.3). In the ~7 year old regeneration forest, Δ200m-15m initially increased during the early morning but then decreased during the early afternoon, usually around 1300 hrs and started increasing again at 1500 hrs (Fig. 3.3). This decrease was observed in all three microclimate metrics (Fig. 3.3), but was particularly pronounced for average temperature (Fig. 3.3A). Whilst the ~45 year old regeneration forest showed a similar pattern to that of the ~27 year old forest, the overall range was highly reduced in this age class for all of the microclimate variables examined. The reduced range in the ~45 year old forest resulted from a highly reduced magnitude of forest influence during the midday period (Fig. 3.3). The magnitude of forest influence during the night was similar for all three age classes, this similarity was particularly strong in average relative humidity and VPD, whilst the magnitude of forest influence at night in average temperature still differed across the age classes, however not to the extent that was observed during the midday period.

The hypothesis that the magnitude of forest influence changed over medium (seasonal) time scales was supported by graphical examination of changes in the magnitude of forest influence with month. Generally the magnitude of forest influence was greatest in January (summer) and lowest in July (winter) (Fig. 3.4). This pattern was observed in both the relative humidity and VPD metrics; however, magnitude of forest influence in temperature showed no distinct pattern (Fig. 3.4A). These patterns were present in all three age classes of regeneration forest. During the winter months (June – August), The magnitude of forest influence approached zero; however, at all stages throughout the year the 15 m plot had microclimate conditions more similar to the mature forest compared to the 200 m plot.

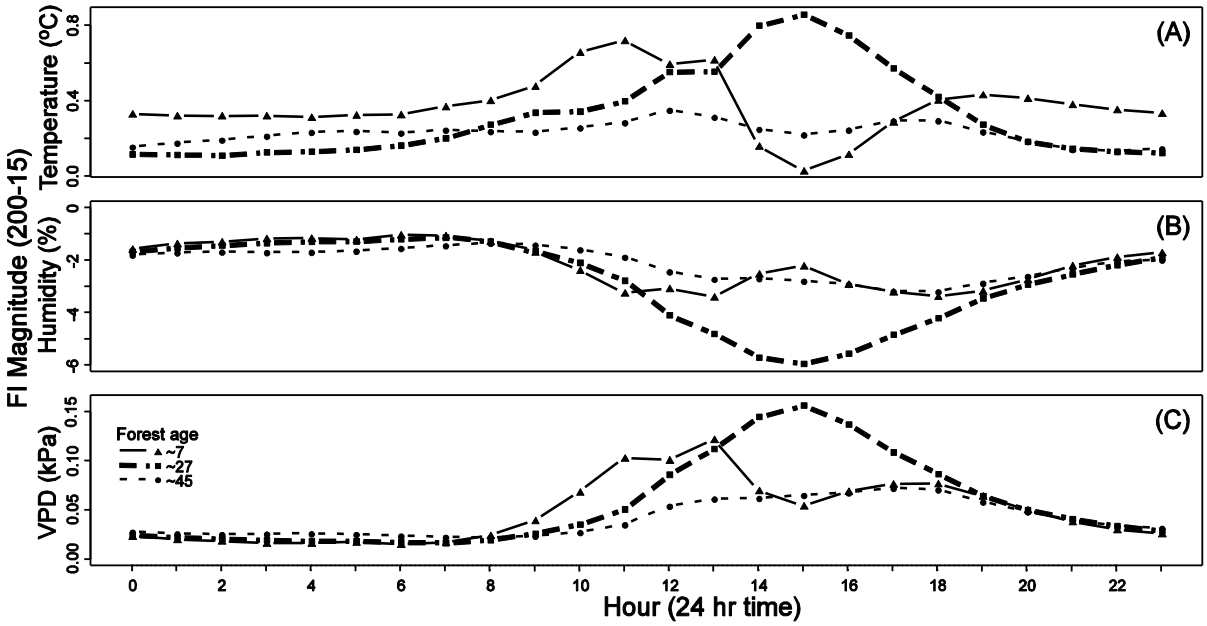

Figure 3.3: Diurnal variation in the magnitude of forest influence (FI) (Δ200m-15m) for each of the three age classes of regeneration forest. Fluctuations in Δ200m-15m are shown for: hourly average temperature (°C) (A), hourly average relative humidity (%) and (B) hourly average vapour pressure deficit (kPa) (C).

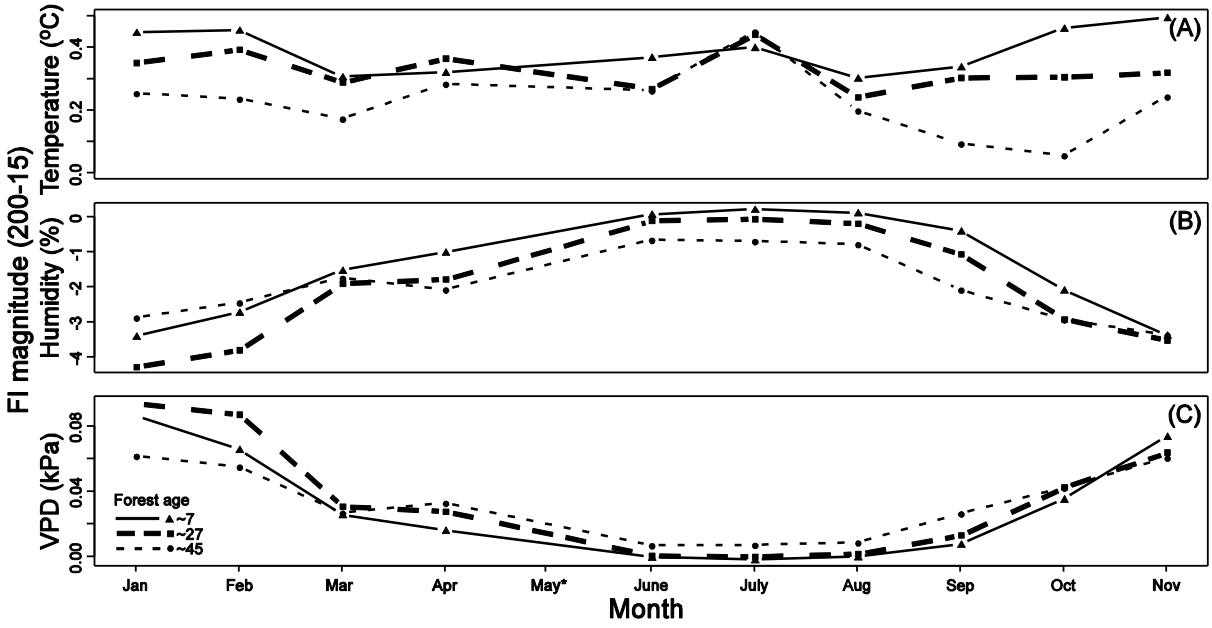

Figure 3.4: Changes in the magnitude of forest influence (FI) (Δ200m-15m) with month. Shows the Δ200m-15m for three microclimate variables in each age class: A) monthly average temperature B) monthly average relative humidity C) monthly average vapour pressure deficit. *Data for May and December were unavailable.

3.4.4. Changes in magnitude with background climate conditions

In accordance with hypothesis 5, the Δ200m-15m was heavily influenced by daily temperature and influenced to a smaller degree by daily wind and rainfall (Table 3.3). Individual regression analyses showed that high daily 3pm temperatures were associated with high absolute values of the Δ200m-15m for daily average temperature ($P < 0.001$), daily average humidity ($P < 0.001$) and daily average VPD ($P < 0.001$). The pattern of response occurred across all three age classes of regeneration forest. An increase in the two-day rainfall reduced the Δ200m-15m for daily average temperature, humidity and VPD ($P < 0.001$) across all three age classes of regeneration forest (Table 3.3).

For average daily humidity and VPD, Δ200m-15m responded to the average windiness of the day in the ~27 ($P = 0.029$) and ~45 year old ($P = 0.045$) regeneration forests, but not in the ~7 year old forest ($P = 0.68$).

Multiple regression of magnitude (Δ200m-15m) against the three daily environmental variables showed that temperature and daily windiness had a significant interaction effect. This was shown for models against forest influence of average daily temperature ($P < 0.001$), daily average humidity ($P < 0.001$) and daily average VPD ($P < 0.001$). Graphical examination (not shown) of this interaction effect showed that the response of Δ200m-15m to daily windiness was small on mild or cold days (under 22°C) and large on hotter days (above 22°C). This pattern occurred for the Δ200m-15m of average daily temperature, humidity and VPD and was consistent across age classes. Other interaction terms (standard daily temperature x amount of rain; amount of rain x standard daily windiness) were shown to be significant for some of the microclimate variables examined; however, these responses were minor compared to the interaction between standard daily windiness and temperature.

Table 3.3: Slopes and P-values for relationships between the forest influence microclimate variables and standard daily environmental conditions. P-values (shown in parentheses) have been Holm-Bonferroni adjusted and significant results are highlighted in bold type. Each test included data from everyday of the summer study period, n =139.

Environmental variable	**Microclimate variable (Δ200m-15m)**	**Regeneration forest age class** ~7	~27	~45
3pm Temperature (°C)	Temperature	0.037 (**<0.001**)	0.049 (<**0.001**)	0.042 (<**0.001**)
	Humidity	-0.235 **(<0.001**)	-0.342(<**0.001**)	-0.235(<**0.001**)
	VPD	0.008 (**< 0.001**)	0.010 (< **0.001**)	0.007 (< **0.001**)
Two-day Rainfall (mm)	Temperature	-0.010 (**<0.001**)	-0.013 (<**0.001**)	-0.010 (<**0.001**)
	Humidity	0.060 (<**0.001)**	0.080 (<**0.001**)	0.047 (**0.007**)
	VPD	-0.002 (<**0.001**)	-0.002 (**0.002**)	-0.001 (**0.003**)
Average Windiness (km/h)	Temperature	-0.002 (0.682)	-0.002 (0.573)	-0.003 (0.314)
	Humidity	-0.031 (0.366)	-0.091 (**0.003**)	-0.064 (**0.009**)
	VPD	0.001 (0.682)	0.002 **(0.029)**	0.001 **(0.045)**

3.5. Discussion

Microclimate in regeneration forests differs from that of mature forests and these differences are particularly strong in younger forest stands. Forest influence on microclimate occurs in our study forests, varies across diurnal and seasonal time scales and changes with succession (peaking in ~27 year old forest then diminishing, although persisting to some degree for at least 45 years).

3.5.1. Microclimate differences between mature and regenerating forests

Forests soon after disturbance have a more xeric and less stable microclimate than mature forests (Fig. 3.2). Other studies also found elevated variability in disturbed forest in temperature (Chen *et al.*, 1993; Strong *et al.*, 1997; Ewers and Banks-Leite, 2013) and to some extent in relative humidity and VPD (Chen *et al.*, 1993; Renaud *et al.*, 2011). Although most of the trends in microclimate differences in young forests continued into older regeneration forests, the magnitude of these differences decreased with forest age. Temperature has been shown to decrease in soils (Ritter *et al.*, 2005) and streams (Quinn and Wright-Stow, 2008; Davies-Colley *et al.*, 2009) with the development of regeneration forests following clearfelling, this indicates that regeneration forest microclimate has the potential to return to pre-disturbance levels. Short-term studies have shown that the recovery of microclimate in forests following harvesting starts within two years of disturbance (Zheng *et al.*, 2000; Guo *et al.*, 2002). However, we found succession of microclimate continuing for at least 45 years after disturbance, although the difference from mature forest at ~45 years is

small. Mature forest microclimate is also influenced by the adjacent disturbance, especially those associated with ~7 year old forest. As we used the microclimate of the mature forest relatively near the edge as a comparison, this may have led to an underestimation of the effect that disturbance can have on microclimate of regeneration forest.

The microclimatic variation in the disturbed forests across the three age classes is most likely driven by differences in LAI, as this was still significantly lower in the ~45 year old regeneration forest than in mature forest. LAI has large impacts on understorey and ground-level microclimate conditions (Murcia, 1995; Davies-Colley *et al.*, 2000; Renaud *et al.*, 2011).

3.5.2. Forest influence on microclimate

Proximity of a mature forest edge is one of multiple factors that affect microclimate within regenerating forests. This supports the findings from the limited number of studies of microclimatic aspects of forest influence (Young and Mitchell, 1994; Cadenasso *et al.*, 1997; Godefroid *et al.*, 2006). Mature forests reduce the level of transmitted light up to one tree-height away from an edge (Huggard and Vyse, 2002; Heithecker and Halpern, 2007), and it is reasonable to predict that these decreased light levels have flow-on effects on other microclimatic variables, as we have shown with the significant microclimate response to LAI.

As differences in microclimate between mature and regeneration forests diminished through time, we expected that the magnitude of forest influence (Δ200m-15m) would also change. Unexpectedly, however, the magnitude and importance of forest influence generally peaked in the ~27 year old forest rather than the ~7 year old forest; but as expected was at it smallest in the ~45 year old regeneration forests (Fig. 3, 4). In the only other previous temporal study on forest influence, Dovčiak and Brown (2014) showed a decrease in magnitude with successional time. However, they only studied two age classes, so could not detect the more complex pattern highlighted by our results. This pattern contrasts with findings from studies of edge effects on forest interiors, which typically have the greatest magnitude immediately after disturbance (Mesquita *et al.*, 1999; Denyer *et al.*, 2006; Wright *et al.*, 2010) before the disturbed forest regenerates and seal the edge (Murcia, 1995; Harper *et al.*, 2005). Further research into temporal aspects of forest influence in other forest systems is required to confirm and elaborate on patterns found in our study. However, results show that there are key differences between forest influence and interior forest edge effects and validates the need to study these processes separately. The peak in the ~27 year old forest is

possibly because Δ200m-15m cannot detect forest influence extending less than 15m from the edge. Thus, at ~7 years, it is possible that microclimatic forest influence may not extend to 15m from the edge. Alternatively, other factors such as canopy cover could be masking the forest influence. It is inappropriate to attribute the microclimatic forest influence observed in the ~27 year old regeneration forest solely to shading from the mature forest, because the regeneration forest has a closed canopy. Instead, diffusion of cold, moist air from the mature forest may contribute significantly (Godefroid *et al.*, 2006). Forest influence persisted at least until ~45 years after edge creation and most likely will not completely disappear until the microclimates of the two forests types are comparable. Due to the large variation between sites in microclimate conditions, attempts at determining the depth of forest influence resulted in wide confidence intervals, and were therefore not presented; further research is required to determine the depth of forest influence on microclimate variables.

While LAI, and to a lesser degree, distance from edge, are strongly related to various microclimate conditions of regenerating forests, heat load and direction to edge are also important in ~45 year old regeneration forest. As shading appears to be an important driver of forest influence on microclimate, edge direction should affect the magnitude and distance because of the greater shading from south facing than north facing edges. Similar patterns have been shown for edge effects into standing forests (Ries *et al.*, 2004; Heithecker and Halpern, 2007), but our study is the first to show this effect on microclimatic forest influence. The potential plot heat load was a strong predictor of microclimate in the ~45 year old regeneration forests. Aspect and slope, both components of heat load, have been highlighted as important factors in influencing the magnitude and depth of edge effects (Redding *et al.*, 2003; Martínez Pastur *et al.*, 2011; Renaud *et al.*, 2011). Because our method of estimating plot heat load does not include all aspects of potential heat load such as topography (Pierce *et al.*, 2005), the effect may have even greater impact than we have shown, and has the potential to influence microclimate in all age classes.

3.5.3. Diurnal and seasonal changes in microclimatic forest influence:

Our observed pattern of forest influence generally peaking in the afternoon is similar to patterns observed for edge effects into mature forests (Chen *et al.*, 1995; Saunders *et al.*, 1999; Davies-Colley *et al.*, 2000; Newmark, 2005) and the impact of streams on forest microclimate (Rykken *et al.*, 2007). The sharp decline in the magnitude of forest influence in the ~7 year old regenerating forests during the afternoon period when the other regeneration forest age classes were generally near their maximum may relate to the absence of a shading

effect, as the sun is at its highest point in the sky. Therefore, the shading distance of the trees will be greatly diminished, and the 15m plot may not be shaded by edge vegetation; thus the difference between it and the 200 metre plot would be reduced. The lack of this effect in the ~27 and ~45 year old regeneration forests may be due to buffering from canopy closure. This potential decrease in midday shading could also help explain the observed differences in magnitude between the age classes.

The magnitude of forest influence is small, but consistently present during the night and early morning. During this period of the day, the microclimatic conditions between the regeneration forest and the standing forests are at their most similar across age classes. This is another case in which forest influence differs from edge effects into mature forest, which typically show strong morning peaks due to light penetration from early morning sun angles (Meyer *et al.*, 2001; Denyer *et al.*, 2006). In contrast, shading from a mature forest would reach hundreds of metres during the early hours of the morning in west facing edges, affecting both the 15 and 200 metre plots, whereas east-facing edges would receive no shade. Furthermore, without a substantial night time difference in microclimate conditions between mature and regeneration forest (Fig. 3.2), the gradient across the edge would be largely nullified. A study into edge effects in Australian tropical forests showed that gradients between forest types were negligible at night (Pohlman *et al.*, 2009), although mature forest can provide higher levels of frost protection during the night (Nunez and Sander, 1981).

The broad patterns in seasonal variation in forest influence, particularly the summer peak, are consistent with patterns in edge effects studies in undisturbed forest (Young and Mitchell, 1994; Silbernagel *et al.*, 2001; Pohlman *et al.*, 2009; Renaud *et al.*, 2011; Ewers and Banks-Leite, 2013). Monthly forest influence magnitude varied least in the ~45 year old regeneration forest, but was consistently above zero, further evidence that forest influence is diminished but still present ~45 years following disturbance. The impact that forest influence had on monthly average afternoon temperature does not follow as a distinct a pattern as for the other two metrics. This may be because afternoon temperature is highly responsive to cloud cover, which fluctuates markedly at any time of the year in Tasmania, whereas relative humidity and VPD respond to moisture levels within the forests which show stronger seasonal patterns. The variation in pattern among microclimate variables highlights that different aspects of microclimate vary in their patterns of forest influence, as has been noted in previous forest influence studies (Young and Mitchell, 1994; Chen *et al.*, 1995; Cadenasso *et al.*, 1997; Cadenasso *et al.*, 2003).

3.5.4. Changes in forest influence with standard daily climate conditions

Daily environmental conditions are strong drivers of changes in the magnitude of forest influence. Edge effects into mature forest increase in magnitude on hot sunny days (Miller, 1980; Chen *et al.*, 1995; Davies-Colley *et al.*, 2000) and our study shows that this is also true to varying degrees for forest influence in temperature, vapour pressure deficit and relative humidity. Davies-Colley *et al.* (2000) and Chen *et al.* (1995) found that edge effect gradients into mature forests are strongest on windy days, however our study shows that windiness only affects the magnitude of forest influence on hot days. The greater importance of wind in forest interior edge effects may be due to wind pushing warmer air into the standing forests (Li *et al.*, 1991), whereas in exposed early aged regeneration forest, wind should mix the air and remove gradients caused by cooler air moving into regeneration from the mature forest. However, extreme daily temperatures seem to override this impact.

The largest values of forest influence all occurred when there was little rainfall in the previous two days. When the regeneration forest is drying out, it appears that the standing forest has the ability to buffer the microclimate of nearby regenerating forest, providing cooler, more humid conditions with lower vapour pressure near edges.

3.5.5. Impact of microclimatic forest influence

Knowledge on how the magnitude of forest influence changes throughout diurnal, seasonal and successional time periods, as well as with daily climate conditions, allows for a better understanding of factors controlling the regeneration of disturbed forests. Changes in microclimate affect a vast range of ecological function, including basic plant functions such as germination and flowering (Bell, 1994; van Doorn and van Meeteren, 2003). As a result, gradients of microclimate with distance from an edge could induce changes in community composition. Changes in species composition have already been shown for vascular and bryophytes in Tasmanian wet forests (Tabor *et al.*, 2007; Baker *et al.*, 2013b). We suggest that these community changes could be driven, at least in part, by the impact that forest influence has on microclimate, although dispersal limitation probably also plays an important role (Baker *et al.*, 2013a). At its strongest, the magnitude of forest influence exhibited by our study reached approximately 0.8 degrees Celsius of temperature or 6% humidity (Fig. 3.3), although these numbers could potentially be greater on hot windy days. These changes may be enough to alter the development or habitat occupancy of a variety of flora and fauna.

Whilst there is potential for all organisms to be affected by forest influence, some species will be more sensitive than others. For example, of the Tasmanian wet forest flora, *Atherosperma moschatum* has a narrower optimum temperature range than most other species (Read and Hill, 1988), so might therefore be impacted more heavily by forest influence. Matching information on species' optimum ranges and the magnitude to which forest influence effects microclimate will allow forest managers to be aware of species which might be aided by management techniques which maximise forest influence. Increased microclimatic forest influence during the summer months means organisms that have important life history stages during summer may be more impacted, especially if these life history stages are particularly sensitive to temperature or humidity. For example, many vertebrates have seasonal peaks in activity (such as species which hibernate or aestivate) while insects commonly exhibit seasonality in life history stages such as egg, larval, adult and pupal stages (Strehlow *et al.*, 2002). Tasmanian saproxylic beetles show a species peak in adult activity during summer (Grove and Forster, 2011); these species may be more forest influenced then the species that are active during winter. The daily periodicity of forest influence could also differentially impact certain species, with nocturnal organisms less likely to be impacted by forest influence, whilst those that are most active during the middle day may be more sensitive. Alternatively, some species may be disadvantaged by forest influence, with changes in microclimate and increased shade resulting in reduced growth (see Baker *et al*. (2013a)).

Microclimatic forest influence may also have substantial effects on abiotic components on ecosystem function. Ecosystem processes such as nutrient cycling are influenced by microclimate conditions (Redding *et al.*, 2003). Also, the greater magnitude of forest influence on hot, windy days, which traditionally are the days with the highest fire danger, may result in regeneration areas exposed to forest influence being somewhat less prone to fire. An important, and perhaps surprising, finding from this study is that forest influence persists for at least 45 years after disturbance, even though these forests are already tall with a closed canopy. This knowledge is relevant for informing decisions about logging rotation lengths, as knowing that older age classes of regeneration forests still benefit from microclimatic amelioration from adjacent mature forest allows managers to factor this into decisions about whether or not to harvest adjoining mature forest.

3.5.6. Conclusions

Forest influence is a contributing factor that impacts the microclimate of adjacent forests regenerating after disturbance. However, the magnitude of microclimatic forest influence varies over temporal scales, and in our system was greatest at an intermediate successional stage, midday and during the summer months. The peak in the intermediate successional stage differs from the current knowledge of temporal aspects of edge effects on interior forests. This highlights that forest influence is a distinct concept and needs to be studied as such.

The impact of the temporal variation of forest influence means that the effects on habitat conditions for forest organisms will vary with time, and may have differential effects on particular species' life history stages. Forest managers implementing retention forestry systems such as aggregated retention, which aims to maximise the harvested area under forest influence (Mitchell and Beese, 2002; Baker and Read, 2011), should be aware that the effect of microclimatic forest influence will not be constant throughout the day, year, over decades and depending on daily climate conditions. These results suggest that if forest influence knowledge is to be applied for a management purpose, the individual species phenology, the local environmental conditions, the length of harvesting rotations and rates of recovery following disturbance all need to be considered.

Chapter 4.
Forest influence on bryophyte recolonisation

This chapter is currently under review in the Journal of Vegetation science as Baker, T.P, Baker, S.C, Dalton, P.J, Fountain-Jones, N.M and Jordan, G.J. Distance to a mature forest impacts the recolonisation of disturbed forest by bryophytes: but does time since disturbance change the impact

In addition to the candidate the development of this experiment was assisted by GJJ, SCB, field work was carried out by the candidate and NMF and the preparation of the manuscript was assisted by GJJ, SCB, PJD, and NMF.

4.1. Abstract

This chapter investigates whether the recolonisation of disturbed forests by bryophytes is impacted by edge effects from a standing mature forest (forest influence). Additionally, this chapter examines if edge effects on bryophytes varies with time since disturbance, by testing if the responses of depth and magnitude of edge effects show different patterns through time.

To determine the response of bryophyte to forest influence, transects were placed across a mature/regeneration forest boundary and bryophyte community composition was recorded from the ground and coarse woody debris at set distances from the edge. A chronosequence of disturbed forest ages (~7, ~27 and ~45 years post disturbance) was used to examine how edge effects changed through time. Models generated by non-linear canonical analysis of principal coordinates (NCAP) predicted the depth of forest influence, and "distances among centroids" inferred the magnitude of forest influence. Magnitude and depth of edge effects were compared across forest ages to determine temporal responses.

Results showed that bryophyte composition in regeneration forests responded to distance from a mature edge. Locations closer to a mature edge had greater similarity in community composition with mature forests. However, the response changed with time since disturbance; the depth of forest influence increased with time since disturbance, and the magnitude of forest influence decreased with time since disturbance. There was a trend for mature forest species to be the most responsive to edge effects however, responses were species specific and varied with forest age.

Distance to a mature forest edge (forest influence) affects the success of bryophytes recolonising after disturbance. This concept has the potential to be used in the design of harvesting units as it can aid the recolonisation of pre-disturbance bryophyte communities. Mature forest associated species tended to respond stronger to edge effects, often these species are at most at risk of being lost after disturbance, further highlighting the need to consider edge effects in management. Finally, this chapter details how studies of edge effects need to consider the metric used and the age of the forest, as depth and magnitude showed opposite patterns in response to forest succession

4.2. Introduction

A key aim of sustainable forest management is to speed up the return of ecological communities to near their pre-harvest state. In the last few decades retention forestry techniques, which retain elements of mature forests within harvested areas, have come to the fore as a way to conserve biodiversity and support the redevelopment of pre-harvest communities (Gustafsson *et al.*, 2012; Lindenmayer *et al.*, 2012). Aggregated retention is a common form of retention forestry (Baker and Read, 2011) and it aims to increase the area of a harvested unit which is under "forest influence". Forest influence refers to edge effects that occur in the harvested matrix near uncut forest (Mitchell and Beese, 2002), as opposed to the more commonly studied edge effects which occur within standing forests (Harper *et al.*, 2005). In this paper we will use 'interior edge effects' to refer to gradients in species composition and/or abiotic conditions within the uncut side of the boundary, and 'forest influence' as gradients within the harvested areas.

Two dominant factors drive the effects that forest influence have on communities; firstly retained forests act as sources of propagules/dispersal units for species which do not survive the disturbance, and secondly, the presence of a mature edge can impact environmental conditions of the regeneration forest (Baker *et al.*, 2013a) and thus indirectly affect species' distributions. Due to these benefits, forest influence increases the re-colonisation ability for a range of taxa, e.g. beetles, fungi, vascular and bryophytes (Tabor *et al.*, 2007; Outerbridge and Trofymow, 2009; Baker *et al.*, 2013b; Fountain-Jones *et al.*, 2015). Bryophytes (mosses, liverworts and hornworts) are known to respond to forest influence and are important to study as they play crucial roles in many aspects of forest ecosystems, such as the uptake and storage of nutrients and soil hydrological processes (Brasell and Mattay, 1984; DeLuca *et al.*, 2002; Lindo and Gonzalez, 2010). Bryophyte species richness can equal, and often exceed, the richness of vascular plants (Jarman and Kantvilas, 1995; Pharo and Blanks, 2000; Dynesius and Zinko, 2006). These contributions to forest health combined with strong responsiveness to disturbance make bryophytes good indicators of mature forest integrity (Frego, 2007).

Managed forests can have lower bryophyte richness than unmanaged forests (Paillet *et al.*, 2010) and differ in their community compositions, thus proactive management may be required to address these differences. There is some empirical evidence that forest influence aids re-colonisation of mature forest bryophytes (Caruso *et al.*, 2011; Baker *et al.*, 2013b),

although Hylander (2009) showed no benefit. Whilst some bryophytes can disperse long distances (Miller and McDaniel, 2004; Sundberg, 2013; Lönnell *et al.*, 2014), the dispersal capacity of species that rarely or never produce spores is often very limited (Miles and Longton, 1992; Kimmerer, 1994; Frey and Kürschner, 2011). The increased proximity to propagule sources associated with forest influence may therefore increase the probability of re-colonisation of disturbed sites, especially for dispersal limited species. However, temporal aspects of re-establishment must be considered, since short distance dispersal may not be limiting over longer time spans. Additionally, bryophyte establishment and growth is limited by microclimate (Busby *et al.*, 1978; Hanslin *et al.*, 2001; Stewart and Mallik, 2006), particularly during germination (Wiklund and Rydin, 2004b). Since the microclimate of disturbed forests varies with distance from a mature forest edge (Davies-Colley *et al.*, 2000; Godefroid *et al.*, 2006; Baker *et al.*, 2014), locations under forest influence may provide better re-establishment conditions for bryophytes.

The impact of forest influence on bryophyte re-colonisation may vary with time since disturbance and seral stage affiliation of the species involved. Bryophytes recolonising immediately after disturbance typically have high dispersal capacities and are tolerant of variable microclimatic conditions (During, 1979; Heinken and Zippel, 2004). Such species may either be little affected by forest influence or even negatively affected near edges. Reduced growth near edges has been observed in some North American pine species (Coates, 2000; York *et al.*, 2003), but this has not previously been investigated for bryophytes. In contrast, many old-growth forest species have limited dispersal ability (During, 1979; Kimmerer, 1994) and are sensitive to microclimate (Busby *et al.*, 1978; Stewart and Mallik, 2006). Whilst these traits may result in high responsiveness to forest influence, mature forest species typically re-colonise during the later stages of forest succession when the magnitude of microclimatic forest influence is diminished (Baker *et al.*, 2014). Therefore, there may be an interesting interaction between species seral stage and the strength of forest influence. However, this interaction is relatively unstudied across all taxa, and to our knowledge, never in bryophytes.

Studies of interior edge effects use both depth (the distance from an edge up to which community composition differs from the normal forest state), and magnitude of edge influence (the size of the difference between edge affected and non edge affected forest) — see Harper *et al.* (2005) for definitions. Most interior edge effects studies focus on depth because it is important when considering the buffering of fragments against disturbance

(Gehlhausen *et al.*, 2000). However, magnitude is also important in understanding the functional impacts of edge effects (Ewers and Didham, 2006). Whilst depth and magnitude of edge influence are often correlated, they can be functionally independent (Harper *et al.*, 2005) and studies have shown that their responses differ in relation to time since disturbance (Matlack, 1994; Dodonov *et al.*, 2013; Dupuch and Fortin, 2013; Dovčiak and Brown, 2014). As studies of forest influence are relatively new, determining the patterns in both depth and magnitude is important.

This paper examines how forest influence impacts bryophyte community composition in forests regenerating after harvesting. It also determines how forest influence on bryophytes changes with time since disturbance. Our specific hypotheses are that:

(1) Bryophytes communities within harvested forests will become more similar to mature forest communities due to proximity to a mature forest edge (forest influence).
(2) The depth of forest influence on bryophyte communities will increase with the age of the regeneration forest, whilst magnitude of forest influence will decrease.
(3) Seral stage will determine species response to forest influence.

4.3. Methods

4.3.1. Study sites

This study was conducted in southern Tasmania, Australia (Fig. 2.1a). Four sites in each of three age classes of regeneration forest were selected: "~7 year old regeneration forests" were harvested between 2002 and 2007; "~27 year old regeneration forests" were harvested between 1983 and 1989 and "~47 year old regeneration forests" were harvested between 1966 and 1972 (plate 1). All sites were regenerating naturally following clearfell, burn and sow silviculture, which involved the use of heavy machinery to harvest all major trees, after which the debris was subjected to a high intensity fire and the area sown with locally-sourced *Eucalyptus* seed. All sites were undisturbed before harvesting and underwent the same harvesting process and were all classed as the same forest type prior to harvesting.

All sites were bordered on at least one edge by mature (undisturbed) forest which contained emergent *Eucalyptus obliqua* and/or *E. regnans* over a rainforest understorey dominated by *Nothofagus cunninghamii* and/or *Atherosperma moschatum*. Species such as *Eucryphia lucida, Phyllocladus aspleniifolius* and *Anodopetalum biglandulosum* were also common. Mature forests were selected which had not been previously harvested and were

undisturbed by wildfire for at least 70 years. Examined edges were selected which did not show any apparent damage to the mature forest from escaped regeneration burns or wind.

4.3.2. Experimental design

Within each site, three transects were established running perpendicular to the mature/regeneration boundary. Transects were placed at a minimum of 50 m apart and ran 35 m from the boundary into the mature forest to 200 m from the boundary on the harvested side. On each transect seven 10 x 10 m plots were marked; two within the mature forest centred at -35 m and -15 m from the boundary ("-" indicates a mature forest plot), and five in the regeneration forest at 15, 35, 70, 120 and 200 m from the boundary (Fig 2.1b). This resulted in 21 plots per site, six in mature forest and 15 within the harvested unit. Two mature forest plots associated with the ~27 year old regeneration forest were not sampled due to subsequent forest harvesting; resulting in a total of surveyed 250 plots.

4.3.3. Bryophyte sampling

The occurrence of bryophyte species within each plot was assessed between January 2012 and May 2013. In each plot, bryophyte community composition was sampled on two substrates: ground and coarse wood debris (CWD) (>10 cm in diameter). Five 10 x 10 cm quadrats were placed for each substrate type within each plot; the individual cover percentage of all species within a quadrat was recorded. Quadrat location was determined by allocating five sampling points within the plot. At each sampling point a quadrat was placed on the closest piece of CWD, and another quadrat was randomly placed on the ground. In cases where the area around the sampling point did not contain a particular substrate, two quadrats were placed at the next sampling point. Seven plots contained less than five pieces of CWD, thus quadrats were placed on the maximum number available.

All bryophytes were identified to species level, except for three genera that may have included multiple species: *Riccardia* (excluding *R. aequicellularis* and *R. cochleata* which were identified to species), *Telaranea* and *Bryum*. Species identification was generally undertaken in the field, but when field identification was not possible, lab-based microscopic identification occurred. Species were identified using published keys for specific genera and where appropriate, Scott (1985) for liverworts and Scott and Stone (1976) for mosses.

4.3.4. Analyses

All species cover data was averaged to the plot level, with plot averages for each species calculated from quadrats on the ground and CWD. Species cover data from CWD and

ground quadrats were combined because many species occurred on both substrates and therefore, combined data gave an overall impression of the response to forest influence. All analyses were conducted in R version 2.15.2 (R development Core Team, Vienna, Austria), unless otherwise stated.

4.3.4.1.Depth of Forest Influence (DFI)

The depth of forest influence on the bryophyte community composition was assessed using non-linear canonical analysis of principal coordinates (NCAP) (Millar *et al.*, 2005). NCAP is an extension of canonical analysis of principal coordinates (Anderson and Willis, 2003), and fitted a nonlinear curve to the gradient in community change (mature to regeneration) in response to distance to boundary. Plot level data was averaged for each distance at each site, resulting in four replicates per distance for each age class, data was then square-root transformed (to give an appropriate weighting to rare species). NCAP was run for each age class based on a Bray-Curtis dissimilarity matrix. Significance of the fit of the NCAP model was determined using 9999 permutations and 95% confidence intervals (CI) were determined by bootstrapping with 1000 permutations. DFI was calculated from the NCAP predicted model as the point where bryophyte community composition was estimated to be 95% similar to the interior regeneration forest community.

4.3.4.2.Magnitude of Forest Influence (MFI)

The magnitude of forest influence (MFI) on bryophyte composition was tested by calculating similarity in species composition between mature forest plots and plots at 15 m and 200 m in the regeneration forest. Similarity between plots was estimated using the 'distance among centroids' procedure in PRIMER v6 PERMANOVA+ (PRIMER-E ltd, United Kingdom). This analysis was run separately for each site using a Bray-Curtis similarity matrix based on square-root transformed data. Centroids were calculated for the 15 and 200 m plots, and for the combined mature plots (-15 and -35 m) plots. The Bray-Curtis similarities between the mature centroid and each distance in the regeneration forest were then calculated using the average distance on the principal coordinate analysis (PCO) axes. ANOVA was used to test if the maximum MFI changed with the age of the regeneration forest. Maximum MFI at each site was calculated by subtracting the MFI of the 200 m plot from the MFI at the 15 m plot (Δ200m-15m). Maximum MFI was calculated this way as it was assumed that the 15 m plot would be under the most forest influence and the 200 m plot would be under the least, therefore the difference between the two would be an indication of the maximum.

4.3.4.3.Successional analysis

The bryophyte community composition of the four forest age classes (~7, ~27, ~45 and mature forest) were compared using PERMANOVA in PRIMER V6. Data for the mature forest included the -35 and -15 m plots adjacent to all regeneration forest age classes. All mature forest plots were combined into one group as it gave a single reference point for the bryophyte communities of the three regeneration forest age classes. Data for the three ages of regeneration forest was restricted to the plots furthest from the edge (120, 200 m). These plots were assumed to represent the typical regeneration bryophyte community i.e. not affected by forest influence. A PERMANOVA was run with 9999 permutations on a Bray-Curtis similarity matrix based on square-root transformed plot-level data. The model had forest age class as a main effect with site as a nested random factor. Graphical presentation of age class differences were generated using MDS.

4.3.4.4.Indicator value as a predictor of response to forest influence

To determine the impact that seral stage had on the response to forest influence, species' indicator values (an assessment of seral stage affinity) were compared to changes in occurrence in relation to distance to forest edge. Indicator species analysis was performed using `indicspecies` version 1.7.1 package (De Cáceres and Legendre, 2009) in R. As with the successional analysis, only mature (-35 and -15 m) and outer regeneration (120 and 200 m) plots were used. All species were assigned an indicator value using the IndVal value (Dufrêne and Legendre, 1997), based on their affinity to mature forest plots. Values were between 0 and 1, with values closer to 1 representing species which are better mature forest indicators.

The relationship between individual species occurrence and distance from mature forest were analysed using logistic regression for each age of regeneration forest. Logistic regression was used to give an estimation of the scale of forest influence based on the probability of species occurrence along the distance gradient (a distinct approach from DFI and MFI). A species was excluded from this analysis if it occurred in less than 10 of the 60 plots of the age class under consideration. Plot level occurrence data from the regeneration forest plots was transformed to presence/absence. To test whether the scale of forest influence was larger for mature forest affiliated species than early colonisers, the slope of the logistic regression was then regressed against species' mature forest indicator value. Regressions were run for combined regeneration forest age classes and separately for each age class. A single outlier was removed from these tests.

4.4. Results

Ninety-six bryophyte species (51 liverworts and 45 mosses) were found within plots across all ages of regeneration forest and the mature forest. Overall species richness did not vary substantially with age, with 55 species found in the ~7 and ~45 year old forests and 62 species in the ~27 year old forests. The mature forest plots contained a total of 76 species.

4.4.1. Depth of Forest Influence (DFI)

Non linear canonical analysis of principal coordinates showed that the community composition of bryophyte communities changed in response to distance from a mature forest edge in all three age classes. DFI increased with forest age, from 14.9 m ($P < 0.001$, 95% CI = 3.2 – 57.6 m) in the ~7 year old forests, to 33.5 m ($P < 0.001$, 95% CI = 3.4 – 130.9 m) in ~27 year old forest, to 64.3 m ($P < 0.001$, 95% CI = 3.2 – 64.3 m) in ~45 year old forest (Fig. 4.1). The transition from mature forest communities to regeneration forest communities was less abrupt in older regeneration forest than in younger forest (Fig. 4.1).

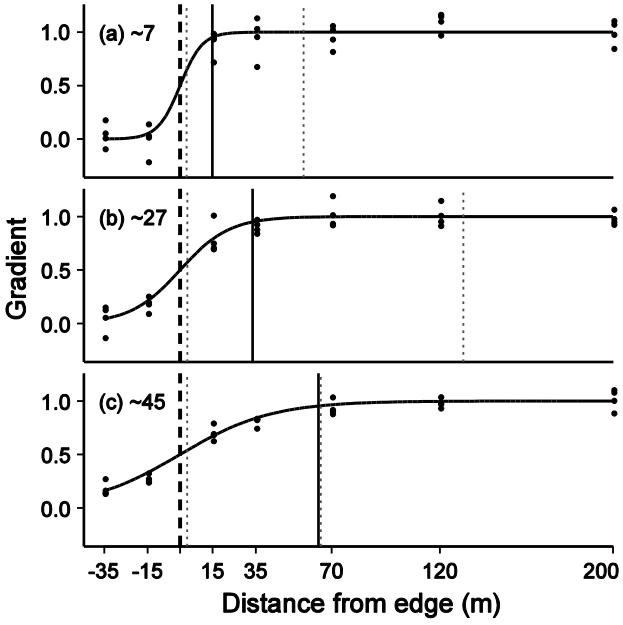

Figure 4.1: Bryophyte community change across mature/regeneration forest boundaries for three ages of regeneration forest; (a) ~7, (b) ~27 and (c) ~45 years old. Models were fitted using non-linear canonical analysis of principal coordinates on bryophyte community data (circles are site replicates, n=4). Gradient is the predicted change in community composition on the Bray-Curtis scale from mature (0) to regeneration forest (1). Solid vertical lines represent the estimated DFI, grey dashed lines are the 95% confidence intervals of the DFI and black dashed lines are the boundary location.

4.4.2. Magnitude of forest influence (MFI)

The maximum MFI (Δ200m-15m) on bryophyte communities was larger in the ~7 year old regeneration forest than in the ~27 and ~45 year old forests (Fig. 4.2), these differences were not significant ($P = 0.262$) due to high variability among sites within age classes. However, in 11 out of 12 sites, bryophyte communities in plots near the edge (15 and 35 m plots) were more similar to mature forest bryophyte communities than the plots far away were (120 and 200 m). A two-sided sign test indicated that this pattern was significant ($P < 0.01$). In general regeneration communities became less similar to mature forest communities with increased distance from the edge in each of the three age classes (Fig. 4.1)

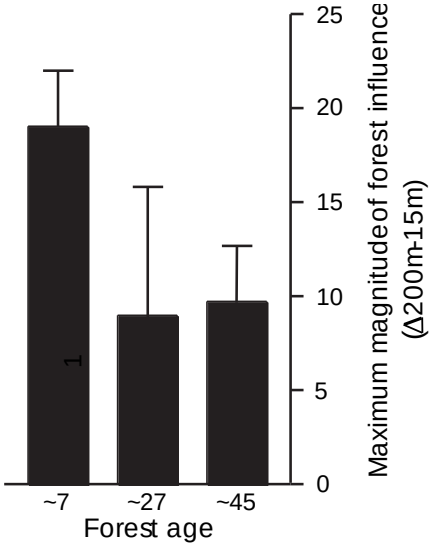

Figure 4.2: Average maximum magnitude of forest influence (± standard error) (n=4). Maximum magnitude was calculated by subtracting the similarity in community composition between the mature and 15 m plot from the similarity between the mature and 200 m plot.

4.4.3. Successional analysis

The ~7 year old bryophyte community was the most distinct group, with smaller differences among ~27, ~45 and mature forest plots (Fig. 4.3). The similarity of regeneration forest communities to mature forest communities increased with age although, pair-wise PERMANOVA tests showed that bryophyte community composition differed between mature and regeneration forests of all age classes (~7: $P = 0.001$; ~27: $P = 0.006$; ~45: $P = 0.043$). Site as a nested factor was also significant ($P < 0.001$), showing that species composition was different between sites within an age class. PERMANOVA comparisons between the three ages of regeneration forest showed that ~7 year old forests had a

significantly different bryophyte community compared to both ~27 (P = 0.029) and ~45 year old (P = 0.030) forests. The ~27 and ~45 year old regeneration forest did not differ (P = 0.175) however, MDS plotting showed grouping according to age class (Fig.4. 3).

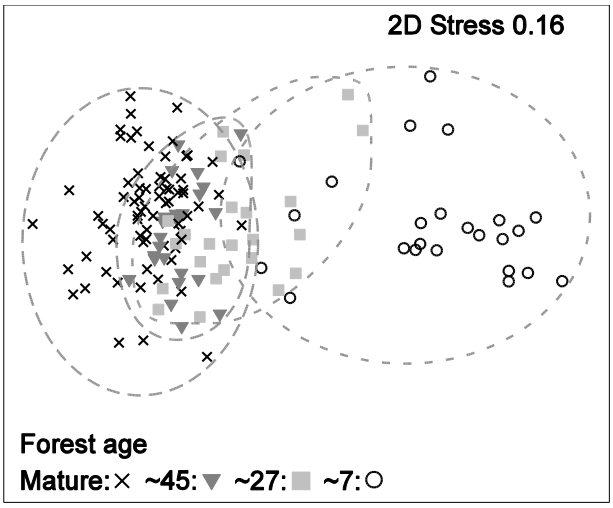

Figure 4.3: MDS ordination plot of the differences in species composition between forest ages. Dotted ellipses encompass the variation of a single age class.

4.4.4. Indicator value as a predictor of response to forest influence

The scale of forest influence on the probability of individual species' occurrences (as predicted by logistic regression) varied among species and regeneration forest age classes (Appendix 2). In the ~7 year old forest, half the recorded species were more common closer to the edge. This increased to 65% in the ~27 year old forest and 60% in the ~45 year old forest (Appendix 2). In the ~7 and ~27 year old forests, species with larger mature forest indicator values showed greater benefits of forest influence based on linear regression of species' mature forest indicator value against logistic regression slopes (Fig. 4a, b). The response was stronger in the ~7 year old forest (slope = 0.028, P < 0.001; Fig. 4a) than in the ~27 year old forest (slope = 0.021, P = 0.011; Fig. 4b). There was no significant response in the ~45 year old regeneration forest (slope = 0.007, P = 0.442), although the trend was similar (Fig. 4c). Forest age had a significant impact on the relationship between indicator value and the scale of forest influence (P = 0.020).

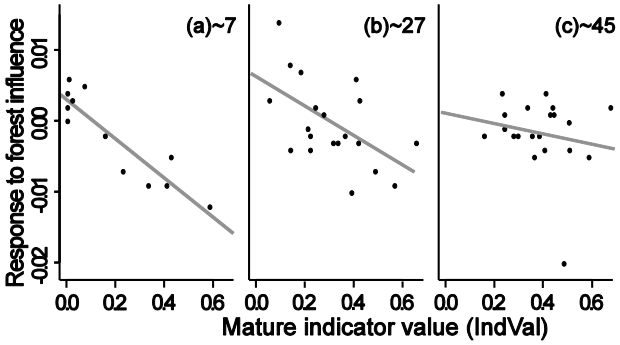

Figure 4.4: Species response to forest influence as predicted by their mature forest indicator value (IndVal). Species response to forest influence was calculated as the slope of the logistic regression of occurrence versus distance from forest edge. Negative values indicate that species were more common nearer a mature forest edge. Mature indicator values (as measured by IndVal) represent the affinity of the species to mature forest. Larger numbers mean the species is a strong predictor of mature forests and occurs frequently in them. Regressions are presented separately for each age class of regeneration forest: (a) ~7, (b) ~27 and (c) ~45 years old.

4.5. Discussion

Bryophyte community composition in disturbed forests is affected by forest influence, with plots near mature forest edges having a bryophyte community that is more similar to communities in mature forests (Fig. 1, 2), this result supported our first hypothesis. Forest influence has previously been shown to aid bryophyte re-colonisation within disturbed forests in Sweden (Caruso *et al.*, 2011) and Australia (Baker *et al.*, 2013b), although other studies have shown no forest influence on bryophytes (Hylander, 2009; Rudolphi and Gustafsson, 2011). Differences in harvesting techniques, aspect and forest type are likely to impact the strength of forest influence, by altering the abiotic and biotic contrasts between mature and disturbed forests. These impacts should be considered in future studies. Dispersal limitations (Kimmerer, 1994; Snäll *et al.*, 2004; Hylander, 2005) and more amenable microclimate conditions next to an edge (Baker *et al.*, 2014) are likely to be the main drivers of the observed community patterns, although the relative role of these factors requires further investigation.

The strong temporal response in both depth and magnitude of forest influence on bryophyte communities (Fig. 1, 2) appears to be the first evidence for temporal variation in forest influence on bryophyte communities, which previously has only been assessed at single points in time (Caruso *et al.*, 2011; Baker *et al.*, 2013b). As we used a chronosequence study, further tests using repeated measures through time would be required to confirm our results. The observed temporal changes in response to forest influence are consistent with

patterns in beetle communities (Fountain-Jones *et al.*, 2015) as well as interior edge effects on bryophytes (Matlack, 1994; Dodonov *et al.*, 2013).

4.5.1. Change in depth and magnitude of forest influence with succession

The change in forest influence with time since disturbance depended on which metric was examined. Results supported our second hypothesis, showing that the depth of forest influence (DFI) increased with age. This follows similar trends to interior edge effects where the depth of edge influence increases with time since disturbance, e.g. for plant growth (Dupuch and Fortin, 2013; Dovčiak and Brown, 2014). The increasing depth of forest influence with time since disturbance is likely driven by a decrease in the magnitude of microclimatic forest influence (Baker *et al.*, 2014) in association with the increased likelihood of bryophytes dispersal through time. For example, if appropriate microclimate conditions were present in both ~27 and ~45 year old forest, we would expect that late-seral species would have dispersed further in the ~45 year old forest due to having greater opportunities for gradual or intermittent dispersal further into the disturbed area with increased time (Baker *et al.*, 2013a). Whilst our results showed a consistent trend of DFI increasing with forest age, the large confidence intervals suggest that variation in the depth of forest influence occurs between sites and further studies are required to confirm our estimations. It is possible that the greater contrast between mature and regeneration communities in young compared to older age classes may have affected the ability to estimate DFI. Whilst we believe that the estimated depths will reflect the point where bryophyte communities have become functionally similar to interior regeneration communities, these issues mean that the temporal variation in depth should be considered with care.

The estimated DFI in the ~7 year old regeneration forest (~15 m) was considerably less than the practical rule of thumb that forest influence extends to a distance equivalent to the tree height of the retained mature forest (Keenan and Kimmins, 1993; Mitchell and Beese, 2002; Baker *et al.*, 2013a), which in this system was 30 - 50 m. However, estimated DFI in the ~27 year old forest (~34 m) was consistent with the one-tree-height rule, and the DFI estimated for the ~45 year old forest in this study was greater (~64 m). This latter result is supported by evidence of a similar DFI for bryophyte communities in another Tasmanian regenerating forest of similar age (Baker *et al.*, 2013b). Indeed, forest influence may still occur in Tasmanian regeneration forest to at least 70 years after disturbance, because bryophyte succession takes at least that long in these forests (Browning *et al.*, 2010). The ~45 year old regeneration forests had significant community differences from the mature forests

and multiple species were observed only in mature forests. DFI for beetle communities on the same sites as the present study also increased with age, although the DFI for beetles (~ 175 m) was higher than for bryophytes in oldest age class (Fountain-Jones *et al.*, 2015). The different response of these two taxa highlights the need to examine forest influence across multiple groups.

The magnitude of forest influence (MFI) on bryophyte communities decreased with time, this confirmed our prediction in hypothesis 2. MFI was greatest in the ~7 year old forest, and was reduced in forests ~27 and ~45 years post disturbance. Decreasing MFI with succession has been documented for forest beetle species (Barnes *et al.*, 2014; Fountain-Jones *et al.*, 2015), but temporal changes in MFI are unknown for other taxa. However, temporal decreases in the magnitude of interior edge effects (Matlack, 1993; Harper and Macdonald, 2002) are typically associated with declining patch contrast (Dodonov *et al.*, 2013; Peyras *et al.*, 2013). A decline in patch contrast was observed in the bryophyte flora of the current study, with regeneration forest communities becoming more similar to mature forest communities through time. Overall maximum MFI may have been underestimated in our study because larger forest influence would be expected between 0-15 m from the forest boundary, which we did not sample.

DFI and MFI showed opposing temporal patterns. For interior edge effects into unlogged forest, the increase in depth with a decrease in magnitude is known as 'edge expansion' (Harper *et al.*, 2005). These temporal and geographical interactions between DFI and MFI are important to consider. For example, looking exclusively at DFI may lead to the conclusions that forest influence is most important in the later ages of the forest, whereas consideration of magnitude can show that, while forest influence affects only a small area of the forest in first few years post disturbance, it does so in a more substantial way.

4.5.2. What types of species respond to forest influence?

Microclimate buffering at the edge (Baker *et al.*, 2014) and the increased proximity to propagule sources provided by forest influence was expected to aid the recolonisation of mature forests species and potentially hinder the recolonisation of early seral species. While mature forest species showed the most positive responses to forest influence patterns (Hypothesis 3, Fig. 4), their stronger response in the early age classes (Fig. 4) suggests that, for mature species, forest influence occurs most in the initial stages of re-colonisation. This shows that forest influence can speed up recolonisation process and recovery of pre-

disturbance communities. As many mature forest species had not yet re-colonised or had low levels of re-colonisation in the ~45 year old forest (Appendix 2), forest influence is likely to still play a role in forests older than 45 years. Additionally, species which were not strong indicators of mature forest tended to be negatively affected by forest influence, particularly in the ~7 and ~27 year old forests. This result was in accordance with other studies suggesting early-seral species may be advantaged by larger openings (Swanson *et al.*, 2011; Baker *et al.*, 2015). Early seral species are generally efficient colonisers of recently disturbed sites and tolerant of the associated environment (Brasell and Mattay, 1984; Meagher and Fuhrer, 2003; Turner *et al.*, 2011). Whilst seral stage affinity was a strong predictor of the scale of the response to forest influence, species-specific variation in responsiveness still occurred. Species-specific responses are also seen in interior edge effects (Moen and Jonsson, 2003; Löbel *et al.*, 2012) and likely occurs due to individual species' dispersal abilities and responses to microclimate. Variation in responses could also occur due to different environmental conditions between substrates on which species occur; further research would be required to differentiate individual substrate responses.

4.5.3. Management Implications & Conclusions

Forest harvesting creates different bryophyte communities compared to forests regenerating following natural disturbances (Ódor and Standovár, 2001; Turner and Kirkpatrick, 2009; Paillet *et al.*, 2010). The ability of forest influence to aid bryophyte community re-colonisation demonstrates that retention of mature forest within and adjacent to harvest units (e.g. with retention forestry approaches (Gustafsson *et al.*, 2012; Baker *et al.*, 2013a)) can help the recovery of bryophyte communities. Areas of retained forest not only increase the area of the harvested unit that is under forest influence (Baker *et al.*, 2013a), but also enable the survival of species that would otherwise be eliminated (Hylander, 2005; Nelson and Halpern, 2005b; Dynesius *et al.*, 2008; Hylander and Weibull, 2012). However, larger gaps will be advantageous for certain early-seral species that have higher probabilities of occurrence further from mature edges. Therefore, management techniques need to consider the impacts that they have on both early and late seral species. An important finding from this study is that the distance and magnitude at which forest influence operates changes over time. Forest influence effects persisted over long time scales (at least 45 years after harvest) suggesting that impacts will persist throughout the length of the harvest rotation period. Furthermore, as bryophytes can be useful forest indicators (Frego, 2007), approaches promoting their re-colonisation may promote the re-colonisation of other taxa.

Chapter 5.
Microclimatic forest influence; a comparison of aggregates and intact forests.

This chapter is in preparation for submission. In addition to the candidate the development of this experiment and manuscript preparation was assisted by Gregory J. Jordan and Susan C. Baker.

5.1. Abstract

Gradients in microclimate are known to exist in harvested forests due to proximity to standing forests; these gradients are often referred to as “forest influence”. Forest influence gradients in microclimate can have a significant impact on the chances of species to recolonise following disturbance. Timber harvesting techniques exist which utilise forest influence in order to improve biodiversity outcomes. One such harvesting method is aggregated retention. This technique involves leaving groups of trees within the harvested area, thus increasing the amount of regenerating forest that is under forest influence. Whilst aggregates are known to produce microclimatic forest influence, differences in the scale of forest influence generated from an aggregate compared to unlogged forests surrounding harvested areas has not been tested. Understanding the ability of retained aggregates to generate forest influence is important in designing and implementing aggregated retention harvesting practices.

This study tested whether the levels of forest influence generated by retained aggregates were the same as those generated by the mature forest surrounding harvested areas. Forest influence was examined by monitoring changes in temperature and relative humidity along a transect running from within standing mature forest, across the boundary, to 60 metres into harvested forest. Transects were located in the direction of maximum expected forest influence (south-facing edges). Results showed that forest influence was similar in both depth and magnitude regardless of the type of forest from which it was generated. Temporal examination of forest influence showed that it changed throughout the day and across the year, with peaks in magnitude occurring during the middle of the day, and in months close to the equinoxes. Temporal patterns in microclimatic forest influence were driven by changes in depth of shade from the standing forest. Due to the importance of shade as a driver of forest influence, this study suggests that the periphery of aggregates may generate less forest influence overall (considering all edge aspects), compared to forests surrounding the harvested areas.

Results from this chapter indicate that aggregated retention is an effective method for generating forest influence within harvested areas. Examining temporal changes highlighted the role of shade in driving microclimatic forest influence in recently disturbed forests. Additionally this chapter showed that at its peak, the microclimatic forest influence will have significant impacts on habitat suitability and thus species recolonisation after disturbance.

5.2. Introduction

Abiotic and biotic gradients between adjacent forest types (edge effects) can impact community composition of plants and animals (Young and Mitchell, 1994; Renhorn *et al.*, 1997; Grimbacher *et al.*, 2006). Most studies on edge effects focus on the deleterious impacts that proximity to a disturbed forest can have on undisturbed forest fragments (Murcia, 1995; Harper *et al.*, 2005). However, undisturbed forests can also create edge effects within adjacent disturbed forests (Mitchell and Beese, 2002) and gradients in this direction are known as "forest influence" (Keenan and Kimmins, 1993). A major component of forest influence is shading by tall mature forest trees creating microclimatic gradients within disturbed forest (Baker *et al.*, 2014). Overall microclimatic forest influence can result in the faster recolonisation of mature forest communities near an edge following disturbance (Tabor *et al.*, 2007; Baker *et al.*, 2013b; Fountain-Jones *et al.*, 2015). Although, other benefits of forest influence, such as reduced dispersal distance compliment the effects of microclimate.

Microclimatic edge effects occur on both sides of a forest edge (Chen *et al.*, 1993; Heithecker and Halpern, 2007; Wright *et al.*, 2010). Microclimatic variation has significant consequences for biodiversity across many taxa (Xu *et al.*, 1997; Stewart and Mallik, 2006) and functional process such as nutrient cycles, water cycles and leaf litter decomposition (Chen *et al.*, 1995; Chen *et al.*, 1999; Riutta *et al.*, 2012). In silvicultural systems, North American pine species have demonstrated reduced growth in areas shaded by a forest edge (Coates, 2000; York *et al.*, 2003) and microclimate/sun exposure is crucially important in eucalypt growth (Battaglia and Sands, 1997). This literature shows that edge gradients can potentially have widespread impacts across forest systems on biodiversity, functional processes and economic potential.

The extent of microclimatic forest influence is of particular importance for forest management. Forest influence gradients in community composition and abiotic conditions can result in the quicker return of pre-disturbance conditions and communities (Baker *et al.*, 2013b; Fountain-Jones *et al.*, 2015). Variable retention (or retention forestry) approaches, such as aggregated retention (where patches of trees are retained within harvested areas), have been developed in order to improve biodiversity outcomes relative to clearcutting. One aim of variable retention is to decrease the average distance of harvested forest to retained forest, this facilitates connectivity and the re-establishment of biodiversity (Franklin *et al.*, 1997; Mitchell and Beese, 2002; Baker *et al.*, 2013a). Forest influence targets are used to

distinguish aggregated retention from clearcutting, for example in Tasmanian forests, retention forestry requires the majority of the harvested area to be within one tree height of standing forest (e.g. aggregates and edges) that will be retained over the long-term (Baker and Read, 2011; Baker *et al.*, 2013a). One tree height is the estimated operating distance of forest influence that is currently adopted by forest managers (Keenan and Kimmins, 1993; Mitchell and Beese, 2002). While one tree height has been shown to be effective in predicting the approximate impact of forest influence on some species and environmental factors (Heithecker and Halpern, 2007; Fountain-Jones *et al.*, 2015), other groups do not respond to this distance (Baker *et al.*, 2013a). Furthermore, recent research shows that the depth of forest influence for both microclimate and biodiversity changes with forest successional recovery (Baker *et al.*, 2014; Fountain-Jones *et al.*, 2015).

Previous studies of forest influence on microclimate have focused on intact edges (edges surrounding the perimeter of the harvested unit, associated with a large amount and length of standing forest) (Redding *et al.*, 2003; Baker *et al.*, 2014). To our knowledge, only Heithecker and Halpern (2007) have examined microclimatic forest influence derived from retained aggregates, and no studies have compared microclimate gradients that originate from aggregates to those that originate from intact edges. Microclimatic forest influence is thought to be driven by two main factors - shading and the flow of air out of mature forest into the disturbed forest (Godefroid *et al.*, 2006; Heithecker and Halpern, 2007). Shading from standing trees has significant impacts on the microclimate of disturbed forests (Young and Mitchell, 1994; Cadenasso *et al.*, 2003). However, microclimatic forest influence can extend past the point of shading (Godefroid *et al.*, 2006) and microclimatic gradients have been observed in disturbed forests with a closed canopy (Baker *et al.*, 2014). This suggests air flow out of mature forests also creates forest influence.

The proportion of edge effected forest is greater within small fragments than larger fragments (Ewers and Banks-Leite, 2013). Therefore, aggregates are more susceptible to interior edge effects altering microclimatic conditions (Cadenasso *et al.*, 1997; Heithecker and Halpern, 2007). As a result retained aggregates may experience different microclimate conditions from intact forests. This could impact the flow of air out of standing forest and thus alter the level of microclimatic forest influence created. Additionally, as intact edges are longer than those provided by aggregates, the penetration of sunlight around the periphery of an aggregate may occur at various times of day. This might result in a reduction in the time that adjacent harvested areas are under shade. Differences in mature forest conditions and

changes in the amount of shade generated between the two edge types could lead to differences in forest influence.

When studying edge effects (both interior edge effects and forest influence), it is important to account for temporal variation (Newmark, 2005; Pohlman *et al.*, 2009; Baker *et al.*, 2014; Dovčiak and Brown, 2014). Microclimatic edge effects are usually stronger during summer (Silbernagel *et al.*, 2001) and the middle of the day (Baker *et al.*, 2014). As the strength of edge effects change temporally, differences between the forest influence generated from an aggregate and that created by an intact edge may also exhibit temporal changes. If shade is a major driver of forest influence, temporal dynamics will be particularly important as the sun angle and direction changes across the day and year. Another important consideration in studying edge effects is the metric used to quantify the effect. Edge effects can be assessed by their spatial scale (depth of edge influence) and the size of the impact (magnitude of forest influence) (Harper *et al.*, 2005; Ewers and Didham, 2006). Depth of influence is commonly quantified (Laurance, 2000; Ries *et al.*, 2004), particularly to determine the spatial scale at which forests are impacted. Magnitude of edge influence describes the extent of the impact and can be used to determine if there will be a functional impact. A comparison of forest influence generated from aggregates and intact forests needs to include both magnitude and depth, as they can be functionally independent (Harper *et al.*, 2005). Thus a lack of difference between edge types in one metric does not rule out a difference in another metric.

This study uses an aggregated retention forest coupe in central Tasmania to investigate whether retained forest aggregates generate microclimatic forest influence (temperature and relative humidity) to the same extent as intact edges. As the drivers of microclimatic forest influence are known to be temporally variable, we will assess the difference between edge types across time periods. We will also investigate the environmental drivers of forest influence in order to shed light on why any potential differences between aggregate and intact edges occur.

5.3. Methods

5.3.1. Study site

This study was conducted at a single site in central Tasmania, Australia (42.58°S, 146.58°E). The site consisted of a harvested forest area (120 ha) surrounding ten retained mature forest aggregates ranging from 1 to 6.5 ha in size (Fig. 5.1a). The harvested area had

undergone clearfell burn and sow silviculture in 2010. The study was conducted between July 2013 and July 2014 when the regenerating forest was three to four years old. The harvested area was surrounded by mature forest with an average canopy height of 36 m, the surrounding forest and the retained aggregates were the same age and forest type. The study site had a small south-facing slope.

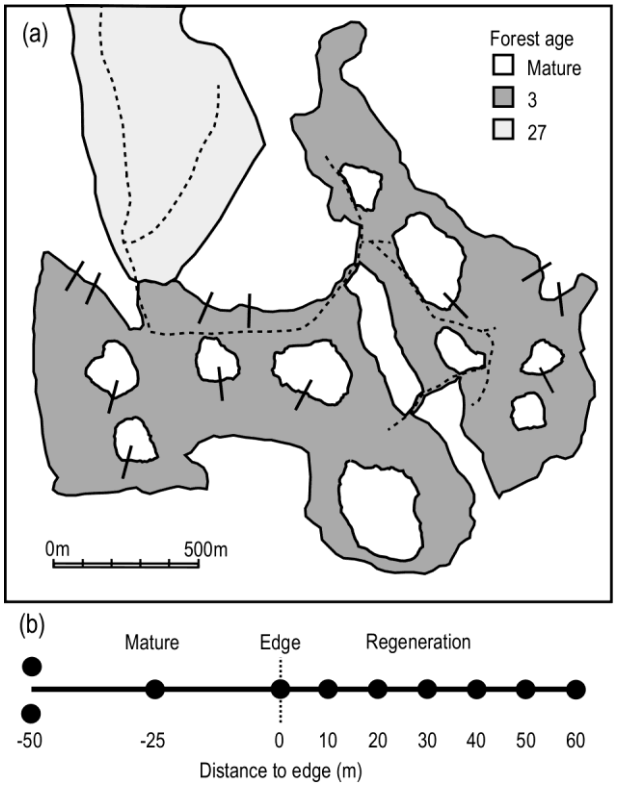

Figure 5.1: (a) Study area showing locations of aggregates and transects. Black lines show approximate transect locations. (b) Transect layout; circles represent locations of a single data logger in relation to distance from the mature/regeneration edge (negative distances indicate mature forest).

5.3.2. Experimental design

Six aggregates and six locations at the surrounding intact mature forest edge were selected (Fig. 5.1a), and a single transect was placed at each location. Transects ran from 50 m within the mature forest to 60 m into the harvested area, perpendicular to the forest edge (Fig. 5.1b). All transects were placed so that they ran approximately north-east to south-west, through to north-west to south-east bearings. This matched the dominant shadow direction and removed edge direction as a confounding factor, as this has a major impact on shade

length and the time of day an area is shaded. HOBO pro V2 temperature/humidity data loggers (ONSET, Massachusetts) were placed at ten locations per transect (Fig. 5.1b). Loggers recorded temperature and relative humidity every 30 minutes for one year. Loggers were housed in solar shields to enable the recording of ambient microclimate conditions and were deployed so recording occurred ten centimetres above the ground. Three loggers were located within the mature forest: two at -50 and one at -25 metres from the edge: seven loggers were placed in the harvested forest at 0, 10, 20, 30, 40, 50 and 60 metres from the edge (Fig. 5.1b). Transects were located where edges had no visible signs of wind or fire damage. In the smallest aggregate, the three loggers monitoring mature forest conditions were all placed 25 metres from the edge.

The site-level environmental variables of solar exposure (a measure of the cloudiness of the day) and daily maximum temperature were derived from the Australian Bureau of Meteorology (BOM) automatic weather stations. Solar exposure was collected at Ellendale (Station No. 095033) and daily maximum temperature was measured at Ouse (Station No. 095048). Solar altitude (angle between sun and horizon) was calculated for the study site at 1215 hours (solar noon) four times a month (7^{th}, 14^{th}, 21^{st} and 28^{th}) using the online calculator at geosciences Australia (http://www.ga.gov.au/geodesy/astro/smpos.jsp).

5.3.3. Analysis

All analyses were conducted in R version 2.15.2 (R Core team, 2012, Vienna, Austria). Temperature and relative humidity data were screened for recording errors; errors were replaced with missing values, although this rarely occurred.

5.3.3.1.Mature forest comparison

Differences in mature forests microclimate between aggregates and intact forest were tested using a two-way fully factorial analysis of variance (ANOVA). Analyses were based on the average microclimate conditions of the -50 m loggers, averages were calculated for each month for both pre-dawn (0400-0700) and afternoon (1300-1600) periods. One of the aggregates was excluded from this test as it did not have -50 m loggers. ANOVAs were run using both mature forest type (aggregates vs. intact forest) and month to test the differences between edge type and variation depending on time of year. ANOVAs were run separately for temperature and relative humidity.

5.3.3.2.Comparing magnitude of forest influence between edge types

Magnitude of forest influence was calculated by subtracting the value of the microclimate metric at the plot 10 m into the regeneration forest from the plot 60 m into the regeneration forest (Δ60m-10m). This approach was taken because the 60 m plot was expected to be under the least amount of forest influence and the 10 m plot under the most. Differences in magnitude of forest influence generated by aggregate and intact forest edges were tested using two-way ANOVAs. Average daily maximum magnitude was calculated per month for each transect, ANOVAs were then run with month included. Differences in magnitude between edge types were also tested using one-way ANOVAs with data restricted to days with extreme environmental conditions. The ten days with the highest maximum temperature, lowest maximum temperature, highest solar exposure and lowest solar exposure were selected using BOM weather station data. For each of these groups, average daily maximum magnitude was calculated for each transect. ANOVAs were then run against edge type. All ANOVAs were run separately for temperature and relative humidity. In addition, differences between edge types were assessed using graphical examination of the temporal responses of depth and magnitude of forest influence as detailed below.

5.3.3.3.Temporal patterns: Magnitude of forest influence

Daily patterns in magnitude of forest influence (Δ60m-10m) were examined by plotting the hourly magnitude for each edge type averaged across transects. Hourly magnitudes per transect were calculated using data across the study period. Patterns in monthly magnitude of forest influence were examined by plotting the average daily maximum magnitude per month averaged across transects. Graphical analyses of the temporal trends were conducted separately for temperature and relative humidity. In addition, a generalised additive model (GAM) of daily maximum magnitude across the year was conducted to assess daily variability in the maximum magnitude of forest influence. GAMs were conducted in the R package `MGCV` version 1.7-29 (Wood, 2011). Daily maximum magnitude was calculated for each day per transect, this data was then averaged for each edge type.

5.3.3.4.Temporal patterns: Depth of forest influence

The depth of forest influence on microclimatic conditions was calculated using non-linear canonical analysis of principal coordinates (NCAP) (Millar *et al.*, 2005). This analysis models the changes in microclimate conditions (from mature to regeneration forest) in response to distance from a boundary. Analyses were run separately per edge type. Changes

in depth of forest influence were assessed across two time periods: firstly, NCAPs were run per hour using the hourly averages of both temperature and relative humidity across the study period; and secondly, analyses were conducted per month using the averages of both temperature and relative humidity from 1100-1200 hours. Individual NCAPs were run by standardising the temperature and relative humidity data and then generating a dissimilarity matrix using Euclidean distance. The NCAP procedure then fits a logistic curve that models how microclimate conditions change between mature and regeneration forests in relation to distance from an edge. The depth of forest influence was assessed as the distance at which microclimate conditions had undergone 95% of the change from mature forest conditions to those found in the regeneration forest. The response of depth of forest influence to both time of day and month were then examined for both edge types.

5.3.3.5. Environmental drivers of forest influence

Site-level environmental factors were tested to determine if they impacted the daily maximum magnitude of forest influence. Data for these tests was restricted to four days a month; 7th, 14th, 21st and 28th. Average daily maximum magnitude was calculated for each transect, then averaged across all transects per edge type. Three environmental variables were used to predict average daily maximum magnitude; solar altitude, solar exposure and the daily maximum temperature. Solar altitude was transformed using absolute value of solar altitude minus 45. A linear regression model of each combination of these factors was tested and the minimum Akaikes Information Criterion (AIC) value determined the most parsimonious model. Models were run separately for temperature and relative humidity and for the two edge types.

5.4. Results

5.4.1. Mature forest comparison

The microclimate conditions of mature forest within retained aggregates were similar to intact mature forest for all measured attributes ($P > 0.642$) except pre-dawn humidity, which was lower in aggregates (aggregate = 95.2%, intact = 96.4%, $P = 0.036$) for this metric there was no interaction with month ($P = 0.211$). For all microclimate measures, the month of recording had a significant impact ($P < 0.001$).

5.4.2. Difference in magnitude between edge types

Edge type did not impact the average maximum magnitude of forest influence for either temperature ($P = 0.820$) or relative humidity ($P = 0.164$). However, month had a

significant impact on magnitude of both metrics ($P < 0.009$). Additionally, the average monthly magnitude of forest influence for temperature ($P > 0.630$) and relative humidity ($P > 0.187$) was similar for both intact and aggregate edges on days with high and low temperature, and high and low solar exposure days.

5.4.3. Temporal patterns: Depth of forest influence

The estimated depth of forest influence varied markedly during the day. It was functionally non-existent from ~ 8 pm until ~5 am, and then rose until the middle of the day (12-1 pm), peaking at 44 m (28-68 m 95% CI) adjacent to intact edges and 35 m (20-60 95% CI) adjacent to aggregate edges. After the midday peak, depth of forest influence decreased, before rising to a secondary peak in the afternoon between 6 and 7 pm (Fig. 5.2). Depth of forest influence then decreased until 8 pm. Both edge types followed the same daily pattern, although intact edges had a higher predicted depth of forest influence during the middle of the day. However, the confidence intervals for the predicted depths of the two edge types overlapped and predicted NCAP models were similar (Fig. 5.2b, c).

Whilst the daily patterns showed that, on average, predicted depth peaked at 36-44 m, monthly patterns in the midday depth of forest influence showed that these depths were greater (≥ 60 m) in March-April and September than other months of the year (Fig. 5.3). However, as sampling only extended to 60 m, actual depths may have been longer. During the colder months (May-August), the depth of forest influence was undetectable using NCAP and is not reported. Whilst intact edges generated slightly longer depths (Fig. 5.3a), the similarity between the models and the overlap in the confidence intervals of the depth estimation suggests these differences are not significant (Fig. 5.3b, c).

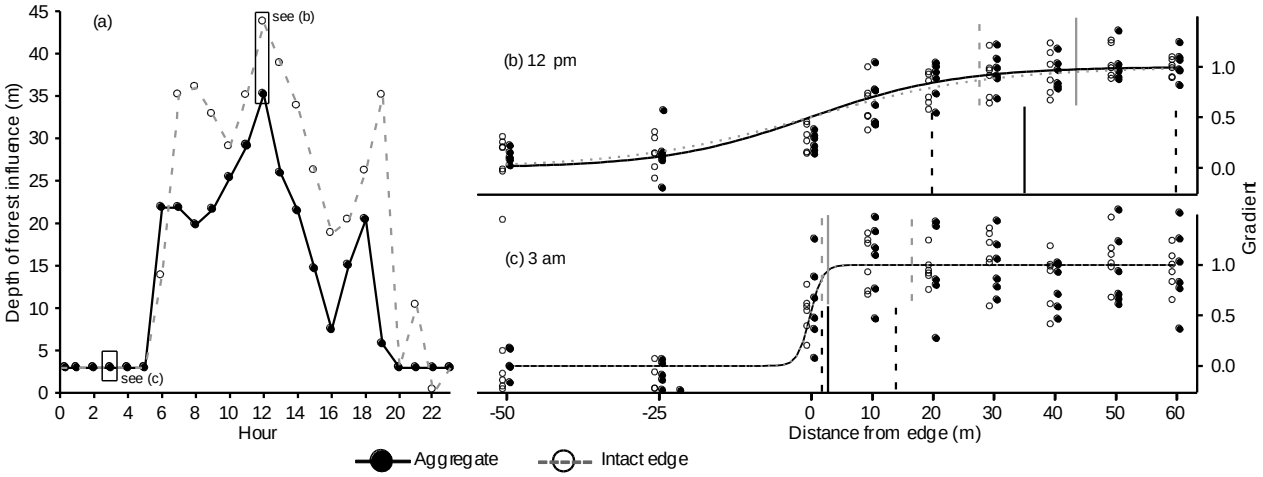

Figure 5.2: Daily patterns in the predicted depth forest influence as calculated by NCAP analysis. (a) Patterns in predicted depth of forest influence over the day; the black lines and filled circles represent sampling adjacent to retained aggregates while the grey dotted line and open circles are samples adjacent to intact edges. (b, c) NCAP logistic models predicting the change in microclimate along the gradient from mature forest conditions (0) to harvested forest interior conditions (1). Predicted depth of forest influence (solid vertical lines) and the 95% confidence intervals (dotted vertical lines) are shown for forest influence off an aggregate (black) and intact edge (grey). NCAP models are shown for microclimate conditions at (b) 1200 hrs and (c) 0300 hrs.

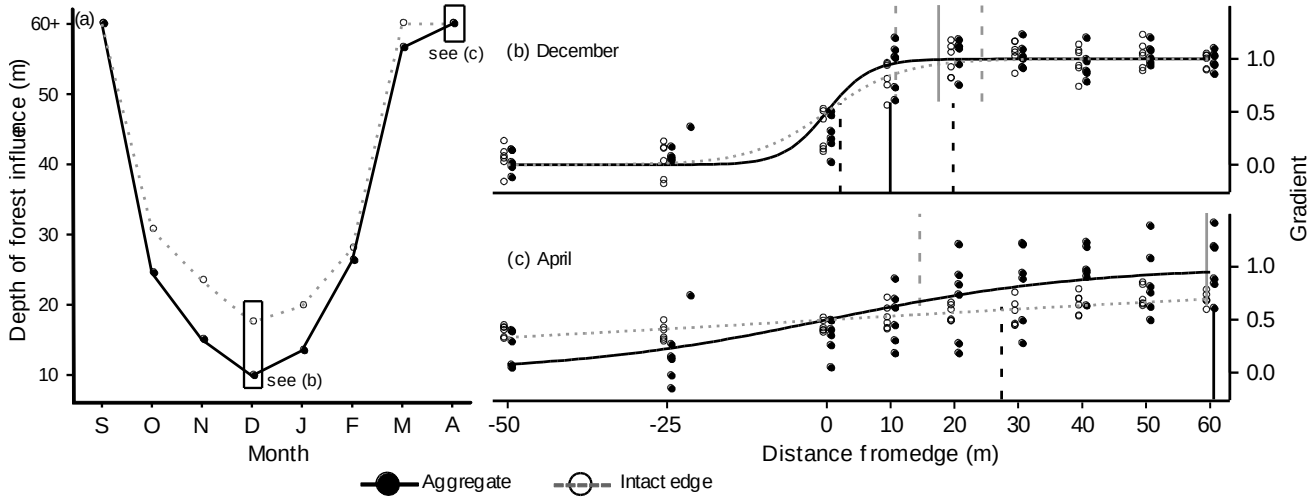

Figure 5.3: Monthly patterns in the estimated depth forest influence as calculated by NCAP analysis. (a) Patterns in depth of forest influence from September to April (depths of May-August could not be predicted by NCAP); the black line and filled circles are predicted depth adjacent to retained aggregates, the grey dotted line and open circles are predicted depths adjacent to intact edges. (b, c) NCAP logistic models predicting the change in microclimate from the mature forest conditions (0) to harvested forest conditions (1) for aggregates (black lines and circles) and intact edges (dotted grey lines and open circles). Predicted depth of forest influence (solid vertical lines) and the 95% confidence intervals (dotted vertical lines) are shown for aggregates (black) and intact edges (grey). NCAP models are shown for (b) December and (c) April.

5.4.4. Temporal patterns: Magnitude of forest influence

There were strong changes in the estimated magnitude of forest influence across the day, with similar patterns for both temperature and relative humidity. Average magnitude was low in absolute terms between late afternoon and early morning, and then increased from around 6 am to a peak at 12 pm (Fig. 5.4). The peak daily magnitude for temperature across all transects of both edge types was 1.24°C (±0.85) and the peak magnitude for relative humidity was 4.19% (±3.11). Magnitude then decreased steadily until 4-5 pm (Fig. 5.4). There were no differences between the daily patterns in magnitude between edge types for temperature; however, the absolute magnitude of forest influence on relative humidity was consistently higher (0.4-1.5%) in transects associated with intact edges (Fig. 5.4b).

Time of year impacted the average daily predicted maximum magnitude of forest influence for both temperature and relative humidity (Fig. 5.5). Patterns for both microclimate metrics were similar, with peak daily maximum magnitude occurring in March (3.98°C, 15.76% RH) and the lowest maximum occurring in July (1.20°C, 4.34% RH). Maximum magnitude also had a second (slightly lower) peak in September (3.12°C, 11.03% RH) (Fig. 5.5). The maximum magnitude of forest influence did not respond to edge type for temperature (Fig. 5.5a). However, for relative humidity, intact edges had a larger maximum magnitude; this difference was more pronounced over the spring to summer period (September-February) (Fig. 5.5b).

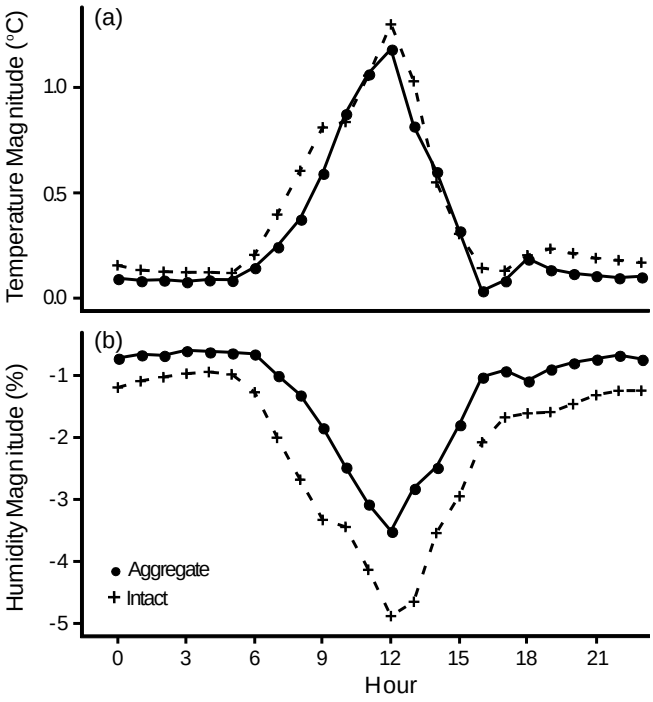

Figure 5.4: Daily patterns in the estimated magnitude of forest influence for aggregate and intact forest edge types. (a) Pattern in magnitude of forest influence for temperature. (b) Pattern in magnitude of forest influence for relative humidity.

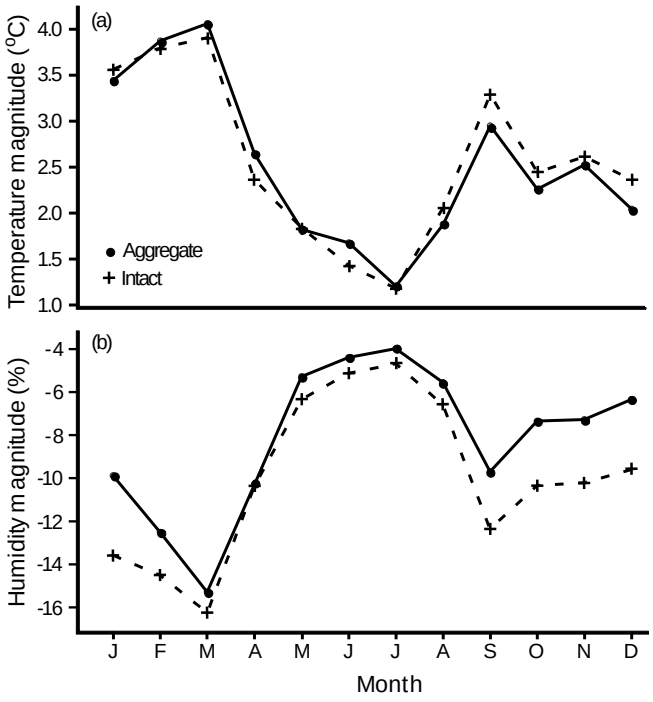

Figure 5.5: Monthly patterns in the average daily predicted maximum magnitude of forest influence for both aggregate edges and intact forest edges. (a) Monthly patterns in the average daily maximum magnitude of forest influence for temperature. (b) Monthly patterns in the average daily maximum magnitude of forest influence for relative humidity.

Generalised additive modelling (Fig. 5.6) confirmed that there were patterns in magnitude over the year for both temperature and relative humidity for both edge types ($P < 0.001$). Patterns in the maximum magnitude were the same for aggregated and intact edges. Peaks in temperature and relative humidity maximum magnitude were observed in both late March and late September; with the March peak larger (Fig. 5.6).

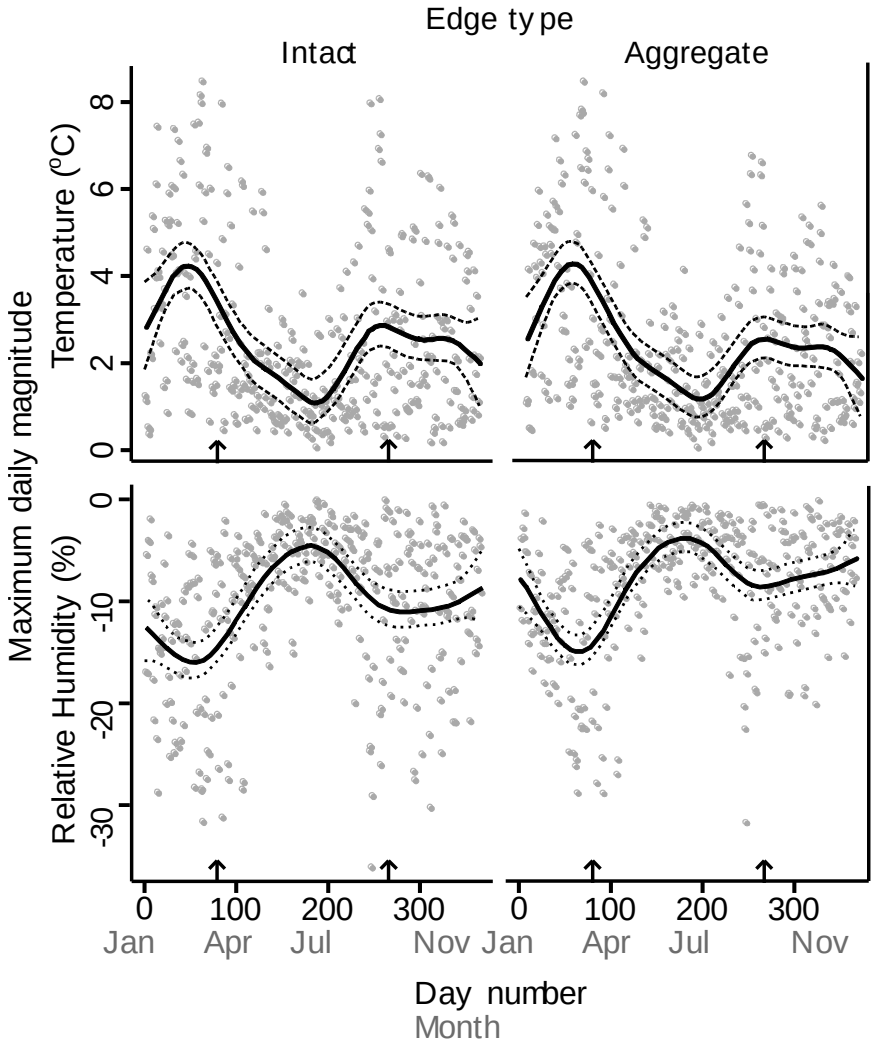

Figure 5.6: Generalised additive model of yearly patterns in the daily maximum magnitude of forest influence for both temperature (°C) and relative humidity (%). Day 0 represents January 1st. GAM models are done individually for forest influence generated by intact and aggregate edges. The black arrow represent the March and September equinoxes.

5.4.5. Environmental drivers of forest influence

The result of the GAMs showed that the dual peaks in maximum magnitude of forest influence occurred close to the equinoxes (when solar altitude is 45°) although scatter occurred throughout the year (Fig. 5.6). Regression models using the landscape-level variables: solar altitude (transformed), daily maximum temperature and solar exposure, showed that all three factors significantly predicted magnitude of forest influence for both temperature and relative humidity. This occurred for both edge types. For temperature, the best model for predicting maximum magnitude included solar altitude and solar exposure, although the model that also included daily maximum temperature had only a slightly larger AIC (Table 5.1). For predicting magnitude of forest influence on humidity, the best model included all terms. For all models tested, the addition of daily maximum temperature and solar exposure improved the ability of solar altitude to predict maximum magnitude.

Table 5.1: Model selection of the best environmental variables used to predict the magnitude of forest influence for both temperature and relative humidity per edge type. The best two models are shown for each combination of edge type and microclimate metric, * represents a term included in the model. Variables tested were sun altitude - 45 (Alt), daily maximum temperature (Max T) and solar exposure (Sol Exp). Values in brackets show the relationship of the response, e.g. (+) indicates that an increase in the environmental variable resulted in an increase in the absolute value of magnitude. For each test n= 48.

	Temperature Magnitude					Humidity Magnitude				
	AIC	R^2	Alt	Max T	Sol Exp	**AIC**	R^2	Alt	Max T	Sol Exp
Agg	179.9	0.424	*(-)		*(+)	283.5	0.454	*(-)	*(+)	
	180.4	0.441	*(-)	*(+)	*(+)	283.6	0.476	*(-)	*(+)	*(+)
Intact	180.9	0.480	*(-)		*(+)	306.5	0.476	*(-)	*(+)	*(+)
	181.4	0.495	*(-)	*(+)	*(+)	309.7	0.416	*(-)	*(+)	

5.5. Discussion

This study showed that standing forests create gradients in microclimate within newly harvested forests. In addition to supporting previous findings of microclimatic forest influence (Huggard and Vyse, 2002; Redding *et al.*, 2003; Godefroid *et al.*, 2006; Heithecker and Halpern, 2007; Baker *et al.*, 2014), we have shown that aggregated retention patch edges generate the same level of forest influence as intact forest edges, at least in the direction of maximum shading. Although levels of forest influence were generally similar, forest influence associated with intact edges had slightly stronger peaks at specific times, especially for relative humidity.

The similar impact of forest influence between edge types may result from importance of shade as a driver of forest influence. The studied harvested area lacked canopy cover; therefore shading from nearby unharvested forest would be an important factor driving microclimatic conditions. Shade in regenerating forests is driven by the height of standing forest, solar altitude, site slope and the direction to the mature forest (Ozdemir, 2008). As this study kept these factors consistent between edge types, little variation in shade would be expected. However, examining differences in estimated shade between aggregates and intact edges (Fig. 5.7) showed that the differences would occur during early morning and late afternoon due to sunlight penetrating around the periphery of retained aggregates. This is when the magnitude of forest influence was low (Fig. 5.4a), therefore differences between edge types would be small and hard to detect. However, the impact of penetration of sunlight around the periphery of aggregates (Fig. 5.7) requires further quantification as data collection from multiple bearings was beyond the scope of this study.

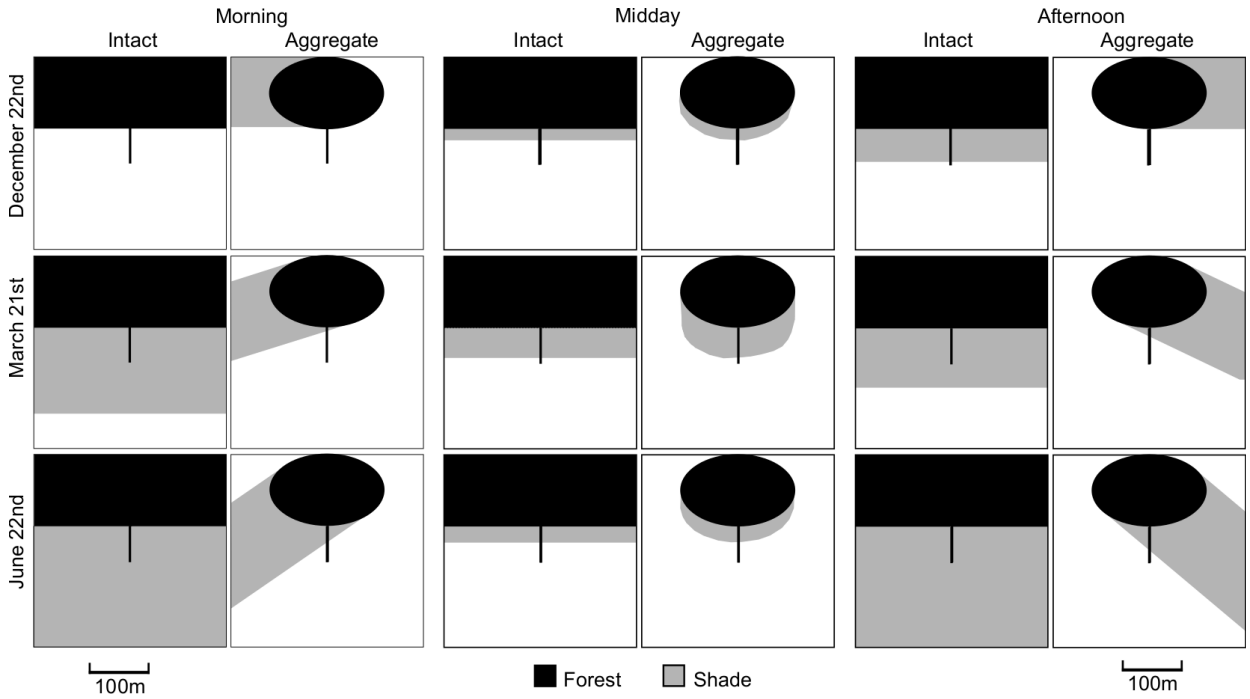

Figure 5.7: The difference in shade between an aggregated and an intact edge. Shading is shown for mornings (8 am), midday (12 pm) and afternoons (4 pm) for three days of the year: December 22nd (summer solstice), March 21st (equinox) and June 22nd (winter solstice). September 23rd (equinox) patterns were the same as the March 21st patterns, so were not illustrated. Black lines represent the studied transect (60 m into harvested area). Shade length was calculated for a forest 36m high.

In addition to shade, similar microclimates between the mature forest of aggregates and intact mature forest are likely to have contributed to the minimal differences in both depth and magnitude of forest influence. Aggregated retention patches preserve mature

microclimate conditions better than other retention types such as scattered retained trees (Heithecker and Halpern, 2006; Rambo and North, 2009). However, this study only examined mature forest microclimate relatively close to the edge (-50 m). As microclimatic edge effects potentially penetrate standing forests to this distance or greater (Chen *et al.*, 1995), there may still be a difference between non-edge effected mature forest interiors and the centre of aggregates. This may have been the case, as the depth of forest influence was consistently higher adjacent to intact edges from 7am to 7pm. Aggregate size will have a significant impact on differences between mature forest conditions, as work on fragmented forest shows that size is directly related to the amount of non-edge effected forest (Laurance and Yensen, 1991; Didham and Ewers, 2012).

Although only relatively minor differences in forest influence generated from aggregates and intact edges were observed, small differences existed during times of peak forest influence, particularly for relative humidity. Air flow from mature forest into the regenerating forest (Li *et al.*, 1991) may be responsible for forest influence extending past the point of shading (Godefroid *et al.*, 2006), as was observed during the middle of the day in the summer months in our study. Higher peaks in forest influence magnitude associated with intact edges could result from the mature forest having a larger volume of air with mature microclimatic conditions than is present within aggregates. Magnitude of forest influence on relative humidity may be more responsive to the flow of moist air out of mature forest and this could explain differences between edge types. However, further research is required to better understand the relative roles of shading and airflow in forest influence.

The strong temporal dynamics in the magnitude and depth of forest influence observed are consistent with other studies of forest influence over daily (Saunders *et al.*, 1999; Baker *et al.*, 2014) and seasonal periods (Young and Mitchell, 1994). Observations of the daily maximum magnitude of forest influence showed two distinct peaks in maximum magnitude (Fig. 5.6); these peaks matched the times of year when sun altitude was closest to 45°. At these two times of year, the angle of the sun together with the tree height of the forest will cast a shadow of around 35 metres (corresponding to the height of the trees), resulting in the 10 m plot being significantly shaded but the 60 m plot not being impacted (Fig. 5.7). Time of peak forest influence will depend on latitude, with higher latitude sites peaking closer to midsummer. For example, forests at 60° latitude will have a maximum solar angle of 45° in early November. Whilst we showed that solar altitude was a very strong driver of forest influence, dual peaks in maximum magnitude within the year were not observed in a

previous study of forest influence in older regenerating forests in the same region (Baker *et al.*, 2014). As those forests had, or were developing, a closed canopy, the impact of shade as a driver of forest influence would have relatively less compared to the present study. In recently disturbed forests, shade will be one of the biggest drivers of forest influence; whereas in older forests, air flow is likely to be the most important driver. Shade is assumed to be the major driver of forest influence in this study because the observed afternoon decrease in magnitude would not be expected to occur if airflow was the major driver.

Whilst solar altitude (shade) was a strong determinant of magnitude of forest influence, high daily variation in magnitude (Fig. 6) suggested that other environmental factors need to be considered. Both daily maximum temperature and solar exposure (a measure of daily cloud cover) mediated the strength of microclimatic forest influence. Daily maximum temperatures are strong drivers of magnitude for both forest influence (Baker *et al.*, 2014) and interior edge effects (Miller, 1980; Davies-Colley *et al.*, 2000). In addition, we found that solar exposure had a strong impact on the daily maximum magnitude of forest influence, with cloudless days resulting in large magnitudes. This effect again suggests that shading is a dominant driver of forest influence in young forests for both aggregates and intact edges.

5.5.1. Conclusions

The observed magnitudes of microclimatic forest in this study were large enough to potentially impact a range of organisms (up to four degrees and 16% RH) (Fig. 5.6). Changes of a few degrees can push plants outside their optimal growth range (Criddle *et al.*, 1997), alter insect communities (Villalpando *et al.*, 2009) and have significant impacts on soil nutrient cycling (Zak *et al.*, 1999). Distance to a forest edge has been previously shown to impact community compositions in regenerating forests (Tabor *et al.*, 2007; Baker *et al.*, 2015; Fountain-Jones *et al.*, 2015), and the microclimatic gradients observed are likely to be one important driver of these responses. Using transects in the direction of maximum shading, we have shown that retained aggregates generate similar depth and magnitude of microclimatic forest influence as intact forest edges. Therefore, these two edge types will possibly have comparable impacts on ecosystem function and community composition. However, as shading was an important driver of microclimatic forest influence, particularly for temperature, differences between edge types may occur in areas where sunlight penetrates around aggregate edges (Fig. 5.7), and the impact of this requires further investigation.

When implementing forest influence as a management tool in harvest layout design, forest managers assume that the depth of forest influence is one tree height (Keenan and Kimmins, 1993; Mitchell and Beese, 2002). This study shows that this estimation can be effective for microclimate, since the average daily peak in depth of forest influence throughout the study period was around 40 metres, compared to the average canopy height of 36 metres. However, there was strong temporal variation in the depth of forest influence. It reached beyond 60 metres during the peak season (midday summer) but was reduced in winter and was non-existent at night. Peak depth correlated with peak magnitude suggesting that the impact of forest influence on ecosystems processes would be high during the warmer months but functionally insignificant during the colder months. Changes in environmental variables between sites such as tree height, altitude, latitude and average temperatures will alter the importance of forest influence. Additionally, the depth and magnitude of forest influence we observed are only relevant for the studied age class, as depths of interior edge effects increase and magnitudes decrease with successional time (Harper *et al.*, 2005; Baker *et al.*, 2014). However, the general mechanisms shown here should be broadly relevant across a range of areas.

Chapter 6.
General Discussion

6.1. Overview

Overall, this thesis aimed to examine the role of forest influence (edge effects into previously harvested forest) in aiding the return of pre-harvest conditions in harvested forests. In particular, I focused on the impact that forest influence had on the return of bryophyte communities and microclimatic conditions. Another focus of this thesis was to determine the interaction between microclimatic forest influence and the responses observed in bryophytes. Finally this thesis was documenting how distance and magnitude of forest influence changed with time. Specifically, the individual chapters in this thesis examined the environmental conditions important for the recolonisation of pre-disturbance bryophyte communities, how microclimate conditions and bryophyte community composition within harvested forests changed due to proximity to a mature forest, and whether aggregated retention silviculture creates microclimatic forest influence to the same degree as forests surrounding a harvested area. Many of these studies used a forest chronosequence so that changes in responses could be observed over the course of forest succession.

In this chapter, findings from the four experimental chapters (Chapters 2-5) are synthesised and discussed in order to determine the impact that forest influence has on the regeneration of harvested forests. In this chapter, I discuss how increasing the maturity of environmental conditions within harvested forests, particularly through forest influence, can result in the faster recolonisation of bryophyte communities. I will then discuss the key drivers of microclimatic forest influence and how results from this thesis can be applied to harvesting techniques, such as aggregated retention. This chapter will also discuss the benefits of examining forest influence across temporal time scales, e.g. daily, yearly and across forest succession. Finally, suggestions will be made on what research is needed to further understand forest influence and enhance its benefits for sustainable forest management.

6.2. Community responses to forest influence

Retention forestry techniques focus on retaining elements of the pre-disturbed forest within harvested areas (Franklin, 1989; Franklin *et al.*, 1997; Pommerening and Murphy, 2004; Kuuluvainen, 2009). These retained structures have been shown to enable the

lifeboating of various species through disturbance (Hannerz and Hånell, 1997; Hazell and Gustafsson, 1999; Caners *et al.*, 2013a; Fedrowitz *et al.*, 2014). However, communities associated with retention can still be markedly different from pre-disturbance communities (Rosenvald and Lõhmus, 2008; Halpern *et al.*, 2012; Johnson *et al.*, 2014; Sverdrup-Thygeson *et al.*, 2014) and retention in association with a reduction in proximity to undisturbed forests is recommended (Oldén *et al.*, 2014). Using bryophytes as a case study, results from this thesis highlight that forest influence is an ecological process that can be used to aid the recolonisation of disturbed forests.

6.2.1. Bryophytes and forest influence

Bryophyte recolonisation following disturbance is a complex process - it depends on numerous factors such as species' dispersal abilities, distance to potential source populations, substrate availability, substrate size and microclimate conditions (Heegaard, 2000; Snäll *et al.*, 2003; Zartman and Nascimento, 2006; Caruso *et al.*, 2011). Results presented in Chapter 2 showed that many environmental factors, and dispersal distance, corresponded with the return of pre-disturbance bryophyte communities. These results suggest that creating mature forest conditions and structures within harvested forests will enable pre-disturbance bryophyte communities to recolonise more effectively. Additionally, the importance of distance to edge and microclimate conditions in determining the maturity level of bryophyte communities suggests that harvesting techniques which utilise forest influence will be efficient in aiding bryophyte recolonisation in Tasmania's wet forests (Chapter 4).

While many factors impact bryophyte recolonisation, this thesis showed that microclimate conditions within disturbed forests had a significant correlation with the recolonisation of pre-disturbance bryophyte communities (Chapter 2). Microclimate has long been established as an important factor that impacts multiple aspects of bryophyte recolonisation/dispersal, e.g. germination (Li and Vitt, 1995; Wiklund and Rydin, 2004b), growth (Wiklund and Rydin, 2004a; Löbel *et al.*, 2012) and reproduction (Rydgren and Økland, 2002; Löbel *et al.*, 2012). Retention harvesting techniques can reduce the impact that harvesting has on microclimate conditions. For example, leaving trees within harvested areas adjusts understorey microclimate levels (Heithecker and Halpern, 2006). Additionally, as shown in Chapters 3 and 5, disturbed areas adjacent to mature forests, both in the form of intact edges and aggregates, have microclimatic conditions more similar to mature forest (Cadenasso *et al.*, 1997; Huggard and Vyse, 2002; Heithecker and Halpern, 2007). Observed results showed that microclimatic forest influence occurs almost immediately after

disturbance (3 years post disturbance, Chapter 5) and persists beyond 45 years post disturbance (Chapter 3). Likewise, forest influence created patterns in bryophyte community composition that generally matched the patterns in microclimate (Chapter 4). For example the forest age with the greatest magnitude of microclimatic forest influence also had the greatest magnitude of forest influence on bryophyte communities (Chapters 3, 4). This adds to the evidence gained from Chapter 2 which shows altering microclimatic within harvested forests has strong impacts on the recolonisation of bryophytes.

Results of the experimental chapters support previous literature which suggests that microclimatic conditions are the key determinants of bryophytes community assembly (Hedenås *et al.*, 2003; Mota de Oliveira *et al.*, 2009; Caruso *et al.*, 2011). However, dispersal distance may still play a critical role in creating the observed forest influence patterns in bryophyte community composition. Distance to a forest edge was a key predictor for many bryophyte communities (Chapter 2) and although patterns in community composition due to edge proximity matched microclimate patterns, it is difficult to untangle the effects of dispersal limitations from microclimatic responses. Bryophyte dispersal follows a strong leptokurtic pattern (Laaka-Lindberg *et al.*, 2003; Pohjamo *et al.*, 2006) which is likely to create the patterns in bryophyte community response observed in Chapter 4. In addition, mature forest species can be the most dispersal-limited (During, 1979) and they tended to be the group most responsive to forest influence (Chapter 4). However, mature forest species are also those most sensitive to variation in microclimate conditions (Proctor, 1990). Further research is required to disentangle the effects of dispersal limitations and microclimate in creating forest influence patterns on bryophyte communities. Due to the estimated similarity in bryophyte community responses to these two factors, it was impractical to assess their individual importance in this thesis.

While the overall bryophyte community showed a significant response to forest influence, Chapter 4 showed individualistic responses of species. Species that were most significantly aided by forest influence included *Gackstroemia weindorferi*, *Heteroscyphus coalitus*, *Podomitrium phyllanthus* and *Cyathophorum bulbosum*. All of these species are known as occurring in older forests (Meagher and Fuhrer, 2003). As mature forest species are known to be more sensitive to the environmental changes associated with forest harvesting and have dispersal limitations (Caners *et al.*, 2013b), it is unsurprising that these species were most advantaged by the microclimatic and dispersal benefits provided by forest influence. Alternatively, species such as *Campylopus introflexus*, *Bryum* spp., *Polytrichum juniperinum*

and *Ditrichum difficile* were all reduced or unaffected by forest influence. These species are known to be efficient colonisers of recently disturbed forests (Brasell and Mattay, 1984; Bradbury, 2006; Turner *et al.*, 2011) and most likely have functional traits such as high caroteniod concentrations and high water retention capacity that allows them to survive high light environments (Rice *et al.*, 2008). Further examination of the functional traits that determine species responses to forest influence would be beneficial as it would shed more light on the relative roles of dispersal and environmental factors in creating forest influence patterns.

6.2.2. Other taxa

At its peak, microclimatic forest influence resulted in significant changes to both temperature and relative humidity (Table 6.1). Therefore, it is important to recognise that impacts of forest influence on community recolonisation will not be restricted to what was observed for bryophytes. Globally, studies across multiple ecosystems show that creating appropriate microclimate conditions aids the restoration of vegetation communities (Yates *et al.*, 2000; Caldwell *et al.*, 2009; Jankju, 2013). In forest systems, microclimate conditions determine species composition and functionality (e.g. growth, breeding, germination niche and habitat suitability) of many taxa including insects (Meyer and Sisk, 2001; Grimbacher *et al.*, 2006) and vascular plants (Criddle *et al.*, 1997; Gehlhausen *et al.*, 2000). It is therefore unsurprising that forest influence has been shown to impact community compositions in both insects and vascular plants (Nelson and Halpern, 2005a; Tabor *et al.*, 2007; Fountain-Jones *et al.*, 2015) as well other taxa such as fungi (Gates *et al.*, 2009). Microclimatic forest influence most likely plays a significant role in establishing these patterns.

Table 6.1: The peak magnitude of microclimatic forest influence over the four age classes examined. Values represent the highest average daily maximum magnitude (calculated per month). *[1] data from Chapter 3, *[2] data from Chapter 5.

Forest age	Temperature (°C)	Humidity (%)
~45*[1]	0.28	-2.88
~27*[1]	0.39	-4.26
~7*[1]	0.45	-3.41
3*[2]	3.98	-15.76

Despite the importance of microclimate, not all taxonomic groups show gradients of forest influence over <200 m spatial scale (Hingston *et al.*, 2014) and even within responsive

taxa, variation between species exists (Baker *et al.*, 2013b; Fountain-Jones *et al.*, 2015). The responses of individual bryophyte species showed that those associated with mature forest are generally the most responsive (Chapter 4). For interior edge effects, species adapted for specialised niches have been shown to the most responsive (Peyras *et al.*, 2013). Changes in responsiveness among species may be due to species-specific tolerance to microclimatic conditions or other drivers of forest influence. Alternatively, variation may result from the observed temporal changes in the strength of microclimatic forest influence (see "Short term temporal changes" below). However, it is important to note that edge effect gradients in one taxa can cascade and result in gradients in related taxa (van Rooyen *et al.*, 2011), therefore species do not have to be directly responsive to the abiotic forest influence gradients.

6.3. Temporal changes in forest influence.

Temporal changes in the strength of forest influence were observed for both microclimatic (Chapter 3, 5) and bryophyte community responses (Chapter 4). For bryophyte communities, temporal changes occurred with forest succession whilst microclimatic forest influence changes were observed with both forest succession and over shorter time periods, e.g. daily and monthly. The temporal changes shown by this thesis provide insights into the mechanism of forest influence and allow us to estimate what types of species will be most benefitted by forest influence processes.

6.3.1. Short-term temporal changes

Microclimatic forest influence showed distinct daily and monthly patterns across all forest ages studied. Previous studies of microclimatic forest influence have suggested that shading from mature forest trees is the major driver of microclimate gradients (Young and Mitchell, 1994; Cadenasso *et al.*, 2003; Godefroid *et al.*, 2006). Therefore, changes in shade that occur throughout the day and across the year would drive temporal changes in microclimatic forest influence. In the three year old forest (Chapter 5) and the seven year old forest (Chapter 3), the magnitude of microclimatic forest influence peaked around midday but was greatly reduced in the early afternoon. The daily patterns of forest influence in these two younger age classes coincided with periods where shading would be at its most important. Additionally, modelling of magnitude over the year (Chapter 5) showed the maximum magnitude was predicted by sun altitude, a major driver of shade (Ozdemir, 2008). Whilst shade was a strong driver of forest influence in young forests, daily patterns in the two older age classes (~27 and ~45 years post disturbance, Chapter 5) suggest the importance of shade

had diminished. In the older age classes, natural forest succession had resulted in canopy closure, therefore additional shade from a standing forest would not have alter conditions significantly. In these cases, the airflow that occurs between forest types (Li *et al.*, 1991) is most likely responsible for generating microclimatic forest influence.

Monthly changes in microclimatic forest influence were observed in both studies (Chapter 3, 5). The magnitude of forest influence tended to be strongest in summer and was diminished during the colder months. Smaller scale edge gradients in winter are consistently observed (for both forest influence and interior edge effects) (Young and Mitchell, 1994; Silbernagel *et al.*, 2001; Pohlman *et al.*, 2009). However, in some other regions, forest influence is stronger in winter due to extreme cold temperatures and snow (Huggard and Vyse, 2002). The diminished microclimatic forest influence in winter observed in the current studies coincides with lower differences in microclimate between mature and harvested forests. Smaller contrasts between forest types are known to limit interior edge effects (Gehlhausen *et al.*, 2000; Denyer *et al.*, 2006; Peyras *et al.*, 2013; Harper *et al.*, 2015) and current results suggest that the same occurs for forest influence. Change in sun altitude was also shown to drive monthly variation in the three year old forest (Chapter 5), yet this was not seen in the older age classes (Chapter 3), possibly due to canopy closure.

Short-term temporal fluctuations in microclimatic forest influence may be responsible for the different responses that are observed across species and taxa (Young and Mitchell, 1994; Baker *et al.*, 2013a). For example, results from this thesis suggest that species with important life history stages during summer will be more impacted then those with important stages in winter. Additionally, nocturnal fauna may be less impacted then diurnal species. Seasonal variation may also have differential impacts on species functional responses. Of particular importance to Australian silvicultural systems, growth of shade-intolerant eucalypts is highly seasonal, peaking in the summer months (Hay *et al.*, 1999; Millner and Kemp, 2012), which coincides with the maxima in the magnitude of microclimatic forest influence.

6.3.2. Changes with succession

As well as short-term temporal changes, both the depth and magnitude (Table 6.1) of forest influence changes with forest succession (Chapter 3, 4). Successional changes in interior edge effects occur for responses of both vegetation (Matlack, 1994; Baldwin and Bradfield, 2010; Dupuch and Fortin, 2013; Harper *et al.*, 2015) and microclimate (Dodonov *et al.*, 2013; Dovčiak and Brown, 2014). However, only recently have studies examined

successional trends in forest influence, e.g. Fountain-Jones *et al.* (2015) for beetles and Dovčiak and Brown (2014) for microclimate. Studies within this thesis detail the oldest known forest to be tested for forest influence patterns (~45 years post harvest) and show that although reduced in magnitude, it is still present for both microclimate and bryophyte communities (Chapters 3, 4). Changes in both bryophytes species composition and microclimate conditions due to forest succession drive the dynamics and persistence of forest influence and are therefore crucial to understand.

Across the three age classes examined for forest influence on bryophytes, the magnitude of forest influence decreased with time since disturbance whilst the estimated depth of forest influence increased (Chapter 4). For microclimatic forest influence, the magnitude of forest influence also decreased with time (Chapters 3, 5) (Table 6.1). This pattern of increasing depth and decreasing magnitude has been observed in studies of interior edge effects (Gascon *et al.*, 2000; Harper and Macdonald, 2002; Harper *et al.*, 2005) and has been termed "edge expansion" (Harper *et al.*, 2005). Studies within this thesis are the first to show edge expansion for forest influence on biological communities (Fig. 6.1).

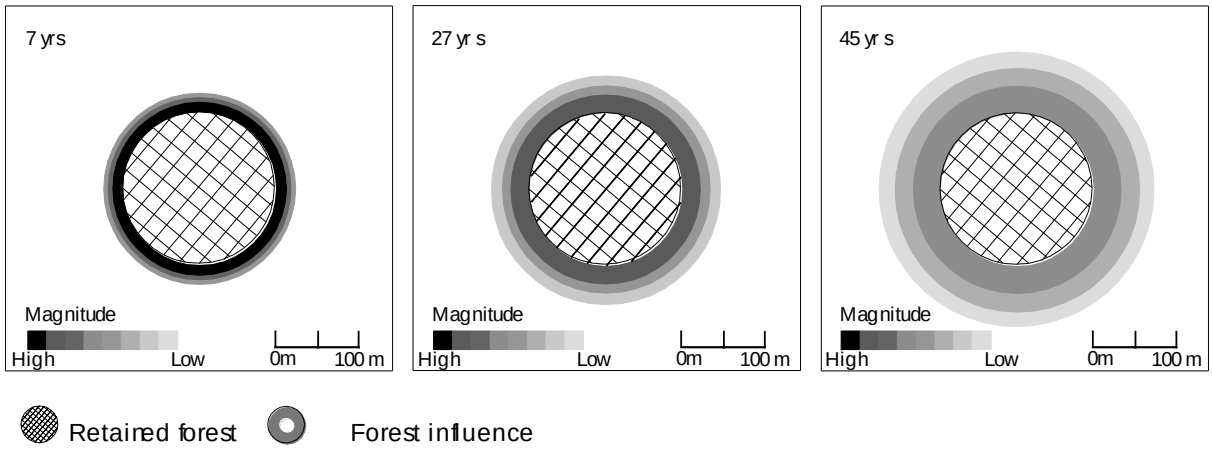

Figure 6.1: The estimated changes in depth and magnitude of forest influence with time since disturbance. Based on observed results from bryophyte communities (Chapter 4).

Successional changes in the magnitude of forest influence are likely due to a reduction in patch contrast, as has been observed for changes in the strength of interior edge effects on both abiotic and biotic elements (Watling and Orrock, 2010; Noreika and Kotze, 2012; Dodonov *et al.*, 2013). Studies in this thesis showed that as the forest aged, both microclimate conditions and bryophyte communities within the harvested forest became more similar to the

adjacent mature forests (Chapters 3, 4). This reduction in contrast between forest types with increasing age of the harvested forest likely led to the consequent decrease in magnitude.

As well as declines in patch contrasts, the reduction in the magnitude of microclimatic forest influence through time may be a driving factor in the reduction in magnitude of forest influence on bryophyte communities. Yet it is important to note that while the magnitude of microclimatic forest influence declined, it still impacted conditions 45 years after disturbance and bryophyte communities also exhibited patterns due to edge proximity in this forest age. In part, the persistence of the bryophyte response in older forests may be due to the sensitivity of mature forest affiliated species. In general, forest specialist species are generally more sensitive to edge effects (Noreika and Kotze, 2012; Peyras *et al.*, 2013) as these species are adapted to more stable environmental conditions. Therefore, the smaller changes in microclimate due to forest influence observed in the oldest forest age classes may still have a significant impact. Indeed, results showed that bryophyte community maturity was most responsive to microclimate in the oldest harvested forest (Chapter 2). In combination with decreasing microclimatic forest influence, the gradual dispersal over time from mature forests may also drive the decrease in magnitude of forest influence on bryophyte communities.

Results from Chapter 4 showed that the depth of forest influence on bryophyte communities increased with age of the harvesting forest (Fig. 6.1). Increasing depth with time since disturbance has been shown for interior edge effects, although this occurs in regions where the disturbed area recovers slowly (Harper *et al.*, 2005; Dupuch and Fortin, 2013) or in forests adjacent to permanently disturbed areas (Gascon *et al.*, 2000). The increase in depths in these circumstances is attributed to the persistent environmental changes gradually changing the community composition. The increase in depth of forest influence observed for bryophyte communities is likely driven by higher recolonisation success when time is included as a factor (Crites and Dale, 1998; Caruso and Rudolphi, 2009). Additionally, the return of pre-disturbance microclimate conditions and the decline in the magnitude of microclimatic forest influence that occur with aging forests (Chapter 3) means that appropriate microclimate conditions will be available further away from the edge.

6.4. Management implications

This thesis shows that bryophyte recolonisation following disturbance is a complicated process that is impacted by multiple environmental factors and has a strong temporal component (Chapters 2, 4). However, development of mature microclimate conditions within

harvested forests had a strong correlation with the re-assembly of pre-disturbance bryophyte communities (Chapter 2) and along with factors such as dispersal distance, is likely to be a key component in bryophyte recolonisation. The impact that forest influence has on microclimate conditions suggests that it is an effective process in aiding the recolonisation of bryophytes and other species (Fountain-Jones *et al.*, 2015). Aggregated retention is a harvesting method that increases the amount of harvested area that is under forest influence (Mitchell and Beese, 2002; Baker and Read, 2011). Results from Chapter 5 support a previous study from Heithecker and Halpern (2007) who showed that retained aggregates can create microclimate forest influence. However, this thesis goes a step further, showing that for transects in the direction of maximum expected forest influence, both the depth and magnitude of forest influence generated by aggregates are very similar to those created by intact forest adjoining harvested areas. However, as noted in Chapter 5, areas adjacent to the periphery of aggregates may receive less forest influence. In these circumstances, an increase in forest influence could be achieved through the use of smaller or irregularly shaped clearfells assuming they are bordered by mature forest. The design of harvested areas to incorporate forest influence processes has the potential to speed up the return of pre-disturbance communities (both bryophytes and other taxa) by adjusting microclimatic conditions within harvested forests.

Implementation of aggregated retention in Tasmania relies on the rule-of -thumb that distance of forest influence is one tree height (Keenan and Kimmins, 1993; Mitchell and Beese, 2002; Baker *et al.*, 2013a). Results from this thesis show that the estimated distance of forest influence is highly dependent on short and long term temporal changes. Therefore, planning for forest influence needs to consider which environmental or biodiversity components are of critical importance for the given forest system and base distances upon their specific responses. However, as shade was the dominant driver of microclimatic forest influence immediately after disturbance, tree height can be a good predictor of the general depth of microclimatic forest influence.

Whilst temporal variation in the depth of forest influence does occur, the magnitude of forest influence on both bryophyte communities and microclimate was greatest during the years immediately after disturbance. Changes in abiotic and biotic conditions in the early stages after disturbance are able to impact the successional trajectory of ecosystems (Noble and Slatyer, 1980; Douma *et al.*, 2012). Therefore, forest influence in the early age classes may be the most important in determining successional pathways and even climax

communities. Thus, despite the variation in depth of forest influence due to the community/environmental factors being examined and the variation through time, the one tree height estimation may be an effective general guideline, as it was similar to the average daily maximum depth of microclimatic forest influence in the youngest forest age class (three years post disturbance, Chapter 5). Nevertheless, responses of bryophyte communities in the youngest age class studied suggested that one tree height may be an over-estimation of the effectiveness of forest influence (Chapter 4). It is important to note that as well as temporal variations in the scale forest influence, variation occurs due to both the variable examined (Chen *et al.*, 1999; Gehlhausen *et al.*, 2000) and the metric (depth compared to magnitude) (Harper *et al.*, 2005). This is an important concept to consider when applying forest influence guidelines for biodiversity management.

Whilst results from this thesis show that aggregated retention has potential for aiding the conservation of bryophyte communities through forest influence, the importance of multiple environmental factors and the variation across substrates (Chapter 2) suggests the importance of other management considerations. For example, on coarse wood debris (CWD), bryophyte communities responded to log decay class and size. Harvested forest can potentially be limited in the quality and quantity of coarse woody debris and therefore CWD requires specific management (Grove and Meggs, 2003). Variation in the response to forest influence in taxa studied concurrently with this thesis, e.g. beetles (Fountain-Jones *et al.*, 2015), birds (Hingston *et al.*, 2014) and vascular plants (Balmer et al. Unpublished data), shows a single management approach does not equally benefit all biodiversity. However, as many species and functional processes respond to microclimate gradients, restoring microclimate conditions within harvested forests should have broad benefits, especially for species affiliated with older forests.

6.5. Future directions

Results of this thesis provide an insight into the impact that forest influence has on both microclimate and bryophyte communities. Much of the information gained from this thesis will be applicable to retention forestry methods used worldwide, particularly aggregated retention. The temporal process and drivers of forest influence, such as shading, should be relatively consistent across forests. However, knowledge gaps still exist in both the understanding of forest influence as an ecological process and the ways it can be

implemented in retention forestry practices. Therefore, more research is required to further refine retention practices, particularly those that utilise forest influence.

6.5.1. Forest influence as an ecological process

Studies in this thesis showed that the recolonisation of bryophyte communities within harvested forests responded to forest influence and that microclimatic changes are likely a major driver of this response. However, other drivers of forest influence, e.g. increased litter input (Fountain-Jones *et al.*, 2015) or competition from mature trees at the edge (Ries *et al.*, 2004), could drive community responses to forest influence. In addition, many environmental factors may interact, which in turn may affect environmental forest influence. In some cases, these interactions clearly lead to increases in the magnitude of forest influence. For example microclimatic changes will have significant impacts on soil functioning (Emmett *et al.*, 2004), which in turn will further affect vegetation dynamics. The key factors which determine the depth of forest influence are difficult to predict. Importantly, dispersal distance may be a key driver of forest influence, particularly for dispersal-limited species. For the bryophyte communities in this thesis, the importance of dispersal distance could not be differentiated from microclimate patterns (Chapter 4). Previous studies of bryophyte recolonisation have used genetic methods (Snäll *et al.*, 2004), spore capturing (Marshall and Convey, 1997) and transplant techniques (Löbel *et al.*, 2012) to determine if dispersal or environmental conditions are limiting recolonisation. These techniques may prove useful in determining the role of dispersal limitations in creating forest influence, not only in bryophytes but other taxa.

As well as variation in forest influence depending on the environmental variable examined (Chen *et al.*, 1999), variation occurs due to landscape-level components. Aspect is major determinant of the strength of edge gradients, both for interior edge effects and forest influence (Chen *et al.*, 1995; Hylander, 2005). In the southern hemisphere, areas on the southern side of a standing forest are assumed to have the largest depths and magnitudes of forest influence as they receive the greatest amount of shade. However, results suggest that the importance of shade driving microclimate forest influence decreases with time since harvest (Chapters 3, 5). This may lead to a decrease in the importance of aspect. Alternatively, as the importance of shade decreases the direction of maximum forest influence may change to match other factors, such as wind direction which drives propagule dispersal.

The benefits of forest influence on the recolonisation of disturbed areas should not be limited to harvested forests. Of studies showing microclimatic forest influence, many documented gradients within agricultural fields (Young and Mitchell, 1994; Cadenasso *et al.*, 1997; Davies-Colley *et al.*, 2000; Li *et al.*, 2007). As microclimatic forest influence is present in these types of systems it has the potential to aid restoration of degraded and disused farmland (Li *et al.*, 2007; You *et al.*, 2010), which is a global conservation challenge (Benton *et al.*, 2003; Wade *et al.*, 2008). In addition, forest influence from natural and managed forests increases the biodiversity values of natural grasslands and therefore improved understanding of the processes which drive forest influence may be of broader benefit for the conservation of these ecosystems (Pryke and Samways, 2012; Ohara and Ushimaru, 2015). In many of these circumstances, the scale of forest influence will be limited by the characteristics of the standing forest. Forest type is suggested as a major driver of the scale of forest influence (Harper *et al.*, 2015), with a smaller contrast between disturbed and standing forests resulting in reduced edge effects (Watling and Orrock, 2010; Peyras *et al.*, 2013; Alignier *et al.*, 2014). Whilst this thesis considered the effect that time since disturbance had on the scale of forest influence, it did not consider the impact that the age and species composition of the mature forest would have. This is an important aspect to consider, especially for the application of forest influence in different forest types and disturbance regimes.

This thesis showed that forest influence impacted bryophyte communities (Chapters 2 and 4). Due to the strength of microclimate forest influence (Chapter 3 and 5), forest influence is also likely to impact numerous other taxa, e.g. beetles (Fountain-Jones *et al.*, 2015). Therefore, forest influence is an important concept to consider when examining community assembly processes following disturbance. Of particular relevance for future forest influence studies is the concept that the way communities assemble can have a significant impact on their function (Fukami *et al.*, 2010). As a result, areas close to an edge may function differently to those further away. Restoring ecosystem function is becoming an increasingly important concept (Montoya *et al.*, 2012) and further studies examining the impact of forest influence on community assembly and function will be beneficial.

6.5.2. Forest influence in management

In this thesis, forest influence was shown to aid the return of pre-disturbance microclimate conditions and bryophytes communities. Additionally, forest influence aids recolonisation of numerous others taxa. Whilst the information provided in this thesis can

help refine the implementation of aggregated retention and other harvesting methods which use forest influence, further research on the role of forest influence in forest management is required to further maximise the biodiversity benefits.

Whilst this thesis showed that aggregates produce microclimatic forest influence (Chapter 5), follow up work is required to determine if aggregates can generate forest influence patterns in community composition e.g. Baker *et al.* (2015). Although, retained aggregates effectively lifeboat bryophytes, and other flora, through disturbance, some species, especially those associated with mature forests, are lost from within the retained patches (Nelson and Halpern, 2005a; Halpern *et al.*, 2012). As a result, forest influence off an aggregate may not have the same impact on community recolonisation as larger areas of mature forest.

This thesis showed that landscape-level environmental conditions impacted the scale of microclimatic forest influence (Chapters 3, 5). Conditions such as high rainfall, low temperatures and areas with low potential heat load limited the scale of forest influence. Therefore, in some ecological contexts, harvested areas with high forest influence may not be as beneficial for biodiversity, e.g. areas with low potential heat load such as south-facing slopes (north-facing slopes in the northern hemisphere), or places with high rainfall. However, in these areas, other drivers of forest influence, e.g. dispersal distance, may still play an important role. Further studies of forest influence are required to understand how and why forest influence varies across the landscape and the flow-on effects this can have for community recolonisation. This will enable managers to determine if forest influence will be effective throughout the landscape.

As this thesis and previous studies have shown, forest influence can have significant effects on the return pre-disturbance ecosystems, thus it has the potential to be an effective concept in the sustainable management of forest systems. However, sustainable harvesting techniques still need to be economically viable (Lafond *et al.*, 2015). Decreases in wood production can occur as a result of forest influence due to factors such as decreased growth rates of crop species near an edge (Coates, 2000; York *et al.*, 2003). However, in Tasmanian wet eucalypt forests, aggregated retention and clearfell areas have been shown to have similar stocking and growth rates for eucalypt regeneration (Scott *et al.*, 2013; Scott *et al.*, 2015). However, areas under forest influence may have additional economic benefits, such as the re-stocking of speciality timbers, e.g. rainforest tree species in Tasmania (Tabor *et al.*, 2007). Some retention forestry techniques can also maintain the potential for a greater range of wood

products in future harvests (Kimmins, 2004). Additionally, retention forestry can be more sociably acceptable (Ford *et al.*, 2009) and if the successful return of pre-disturbance forests using forest influence can be demonstrated, social acceptability may increase. Studies into the economic benefits of techniques such as aggregated retention may provide extra incentive for implementation in the future.

6.6. Conclusions

This thesis investigated the role that forest influence plays in returning pre-disturbance communities and conditions to harvested forest, specifically looking at bryophytes and microclimate. Importantly, the impact of forest influence was examined across four different time periods allowing conclusions to be drawn about the key drivers of forest influence and how the response of communities changes through time.

Studies showed that the return of pre-disturbance bryophyte communities is a complex process, yet forest influence has the potential to reduce the ecological impact of two of the main limitations (microclimate and dispersal distance). The scale of the impact of forest influence on microclimatic conditions is expected to have significant impacts on the recolonisation of many pre-disturbance communities. Results from this thesis showed that this was the case for bryophyte communities. Areas next to a mature forest edge had bryophyte communities that were more similar to mature forest than areas further away from the edge. This has important implications for forest management, as harvested sites with large areas adjacent to mature forest will recover quicker following harvesting.

Finally this thesis showed that forest influence on microclimate can be created adjacent to small islands of retained forests. This shows that techniques such as aggregated retention will increase the harvested area that is under forest influence, thereby providing an important mechanism to aid the return of pre-disturbance bryophyte communities, and potentially many other biological communities.

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Appendix 1

Appendix 1: List of bryophyte species recorded in Chapter 2. Names of mosses are derived from the AusMoss catalogue at the Royal Botanic Gardens, Melbourne (http://www.rbg.vic.gov.au/dbpages/cat/index.php/mosscatalogue/browse/A). Names of Liverwort species are derived from the Department of the Environment and water Resources checklist of Australian Liverworts and Hornworts (http://www.anbg.gov.au/abrs/liverwortlist/liverworts_a_z.html). All names were current at the time of publication. 'X' indicates the species was found in the listed age class (M is the combined mature forest adjacent to all ages of regeneration forests).

Moss Species	**~7**	**~27**	**~45**	**M**
Achrophyllum dentatum (Hook.f. & Wilson) Vitt & Crosby	x	x	x	x
Brachythecium rutabulum (Hedw.) Schimp.	x		x	x
Bryoerythrophyllum dubium (Schwägr.) P.Sollman	x	x		
Bryum spp.	x	x		x
Camptochaete arbuscula (Sm.) Reichardt var. arbuscula	x	x	x	x
Camptochaete deflexa (Wilson) A.Jaeger		x		x
Campylopus clavatus Wilson	x	x		
Campylopus introflexus (Hedw.) Brid.	x	x		x
Campylopus pyriformis (Schultz) Brid.	x	x		x
Catagonium nitens (Brid.) Cardot ssp. nitens			x	
Ceratodon purpureus (Hedw.) Brid.	x	x		
Cyathophorum bulbosum (Hedw.) Müll.Hal.	x	x	x	x
Dicranoloma billarderii (Brid.) Paris	x	x	x	x
Dicranoloma dicarpum (Nees) Paris	x	x	x	x
Dicranoloma menziesii (Taylor) Renauld	x	x	x	x
Dicranoloma robustum (Hook.f. & Wilson) Paris	x	x	x	x
Didymodon torquatus (Taylor) Catches.	x			
Distichophyllum crispulum (Hook.f. & Wilson) Mitt.		x		x
Distichophyllum microcarpum (Hedw.) Mitt.			x	x
Distichophyllum pulchellum (Hampe) Mitt.	x	x	x	x
Ditrichum difficile (Duby) M.Fleisch.	x	x	x	x
Fissidens pallidus Hook.f. & Wilson var. pallidus	x	x	x	x
Fissidens taylorii Müll.Hal. var. taylorii	x			
Fissidens tenellus Hook.f. & Wilson var. tenellus	x	x	x	x
Funaria hygrometrica Hedw.	x			
Glyphothecium sciuroides (Hook.) Hampe	x	x		x
Goniobryum subbasilare (Hook.) Lindb.		x	x	x
Hypnodendron vitiense ssp. australe Touw				x
Hypnum chrysogaster Müll.Hal.	x	x	x	x
Hypnum cupressiforme Hedw. var. cupressiforme	x		x	x
Hypopterygium tamarisci (Sw.) Brid. ex Müll.Hal.	x	x	x	x
Lembophyllum divulsum (Hook.f. & Wilson) Lindb.		x		x
Leptotheca gaudichaudii Schwägr. var. gaudichaudii	x	x	x	x
Leucobryum candidum (P.Beauv.) Wilson	x	x	x	x
Lopidium concinnum (Hook.) Wilson		x	x	x
Mniodendron comosum (Labill.) Lindb. ex Paris		x	x	x
Polytrichum juniperinum Hedw.	x	x		
Ptychomnion aciculare (Brid.) Mitt.	x	x	x	x
Pyrrhobryum mnioides (Hook.) Manuel				x
Racomitrium crispulum var. tasmanicum (Hampe) E.Lawton		x		
Racopilum cuspidigerum (Schwägr.) Ångstr. var. cuspidigerum		x	x	x
Rhaphidorrhynchium amoenum (Hedw.) M.Fleisch. var. amoenum	x	x	x	x
Rhizogonium distichum (Sw.) Brid.	x	x	x	x

Rhizogonium novae-hollandiae (Brid.) Brid.	x	x	x	x
Rhynchostegium tenuifolium (Hedw.) Reichardt	x	x	x	x
Rosulabryum billarderii (Schwägr.) J.R.Spence	x	x	x	x
Thamnobryum pumilum (Hook.f. & Wilson) Nieuwl.		x	x	x
Thuidiopsis furfurosa (Hook.f. & Wilson) M.Fleisch.		x		
Thuidiopsis sparsa (Hook.f. & Wilson) Broth.	x	x	x	x
Wijkia extenuata (Brid.) H.A.Crum	x	x	x	x

Liverwort Species	**~7**	**~27**	**~45**	**M**
Acromastigum colensoanum (Mitt.)		x	x	x
Acromastigum mooreanum (Steph.)				x
Anastrophyllum schismoides (Mont.) Steph.				x
Aneura alterniloba (Hook.f. & Taylor)		x		
Balantiopsis diplophylla (Hook.f. & Taylor) Mitt.	x	x	x	x
Bazzania adnexa (Lehm. & Lindenb.) Trevis.	x	x	x	x
Bazzania monilinervis (Lehm. & Lindenb.) Trevis.				x
Cephaloziella exiliflora (Taylor) Douin	x	x		x
Cephaloziella hirta (Steph.) R.M.Schust.	x	x		
Chiloscyphus latifolius (Nees) J.J.Engel & R.M.Schust.	x	x		x
Chiloscyphus multipennus (Hook.f. & Taylor) J.J.Engel & R.M.Schust.		x	x	x
Chiloscyphus muricatus (Lehm.) J.J.Engel & R.M.Schust.		x	x	x
Chiloscyphus semiteres (Lehm. & Lindenb.) Lehm. & Lindenb.	x	x	x	x
Chiloscyphus villosus (Mitt. ex Steph.) J.J.Engel & R.M.Schust.	x	x		
Cyanolophocolea echinella (Lindenb. & Gottsche) R.M.Schust.	x	x	x	x
Eotrichocolea polyacantha (Hook.f. & Taylor) R.M.Schust.				x
Frullania spp.		x	x	x
Gackstroemia weindorferi (Herzog) Grolle		x	x	x
Heteroscyphus biciliatus (Hook.f. & Taylor) J.J.Engel		x	x	
Heteroscyphus billardierei (Schwägr.) Schiffn.				x
Heteroscyphus circumdentatus (W.Martin & E.A.Hodgs.) J.J.Engel & R.M.Schust.				x
Heteroscyphus coalitus (Hook.) Schiffn.	x	x	x	x
Heteroscyphus cymbaliferus (Hook.f. & Taylor) J.J.Engel & R.M.Schust.				x
Heteroscyphus fissistipus (Hook.f. & Taylor) Schiffn.	x	x	x	x
Heteroscyphus knightii (Steph.) Grolle		x	x	x
Heteroscyphus limosus (Carrington & Pearson) Schiffn.		x	x	
Heteroscyphus varians (Steph.) J.J.Engel,				x
*Hymenophyton flabellatum (*Labill.) Dumort. ex Trevis.		x	x	x
Isotachis intortifolia (Hook.f. & Taylor) Gottsche	x	x		
Kurzia compacta (Steph.) Grolle				x
Lepicolea scolopendra (Hook.) Dumort. ex Trevis.				x
Lepidozia glaucophylla (Hook.f. & Taylor) Taylor ex Gottsche, Lindenb. & Nees			x	x
Lepidozia laevifolia (Hook.f. & Taylor) Taylor ex Gottsche, Lindenb. & Nees		x	x	x
Lepidozia ulothrix (Schwägr.) Lindenb.	x	x	x	x
Leptophyllopsis laxus (Mitt.) R.M.Schust.				x
Marchantia berteroana Lehm. & Lindenb.	x			
Marsupidium surculosum (Nees) Schiffn.	x		x	x
Megaceros spp.				x
Metzgeria furcata (L.) Dumort.				x
Plagiochila fasciculata Lindenb.	x	x	x	x
Plagiochila retrospectans Nees			x	x

Plagiochila strombifolia Taylor ex Lehm.				x
Podomitrium phyllanthus (Hook.) Mitt.	x	x	x	x
Radula buccinifera (Hook.f. & Taylor) Taylor ex Gottsche		x	x	x
Riccardia aequicellularis (Steph.) Hewson	x	x	x	x
Riccardia cochleata (Hook.f. & Taylor) Kuntze	x	x	x	x
Riccardia spp.	x	x	x	x
Saccogynidium decurvum (Mitt.) Grolle,				x
Schistochila lehmanniana (Lindenb.) Steph.		x	x	x
Schistochila pseudociliata R.M.Schust.				x
Symphyogyna podophylla (Thunb.) Mont. & Nees	x	x	x	x
Telaranea spp.	x	x	x	x
Treubia tasmanica R.M.Schust. & G.A.M.Scott		x	x	
Trichocolea mollissima (Hook.f. & Taylor) Gottsche		x	x	x
Tylimanthus diversifolius E.A.Hodgs.		x	x	x
Tylimanthus pseudosaccatus Grolle,			x	x
Zoopsis argentea (Hook.f. & Taylor) Hook.f. ex Gottsche	x	x	x	x
Zoopsis leitgebiana (Carrington & Pearson) Bastow	x	x	x	x

Appendix 2

Appendix 2: Results of indicator species analysis and logistic regression against distance to a mature forest edge. IndVal represent the affinity of a species to an age class, with numbers closer to 1 being a stronger indicator of that age class. Response to distance represents the slopes of logistic regression models testing the presence-absence data of species versus distance away from the mature forest. Bold numbers indicate that *P* <**0.050** and italic numbers represent results with *P* <*0.100,* na represents species that could not be tested due to insufficient numbers.

	IndVal				response to distance		
Species (moss)	Mature	~45	~27	~7	~45	~27	~7
Achrophyllum dentatum	0.237	0.390	**0.427**	0.052	-0.003	-0.002	na
Didymodon torquatus	0	0	0	0.129	na	na	na
Brachythecium rutabulum	0.016	0.099	0	0.152	na	na	na
Bryoerythrophyllum dubium	0	0	0	**0.387**	na	na	na
Bryum Spp.	0.020	0	0	**0.569**	na	na	**0.008**
Camptochaete arbuscula	0.047	0.051	*0.297*	0.031	na	na	na
Camptochaete deflexa	0.088	0	0.124	0	na	na	na
Campylopus clavatus	0	0	**0.275**	0.056	na	na	na
Campylopus introflexus	0	0	0.057	**0.786**	na	na	**0.014**
Campylopus pyriformis	0.040	0	0.214	0.223	na	na	na
Ceratodon purpureus	0	0	0	**0.365**	na	na	na
Cyathophorum bulbosum	**0.359**	0.282	0.070	0	*-0.007*	na	na
Dicranoloma billarderii	0.331	0.340	**0.441**	0.157	*0.005*	-0.002	**-0.011**
Dicranoloma dicarpum	0.154	0.251	**0.385**	0.107	0.002	**0.012**	*-0.006*
Dicranoloma menziesii	**0.547**	0.102	0.171	0.068	na	na	na
Dicranoloma robustum	0.108	0.117	*0.340*	0.091	na	**0.009**	na
Distichophyllum pulchellum	0.196	*0.311*	0.105	0	na	na	na
Ditrichum difficile	0	0.019	0.119	**0.357**	na	na	0.006
Fissidens pallidus	0.119	0.218	0.054	0.077	na	na	na
Fissidens tenellus	0	0.172	0.107	0.110	na	na	na
Funaria hygrometrica	0	0	0	**0.258**	na	na	na
Glyphothecium sciuroides	0.131	0	0.035	0.144	na	na	na
Goniobryum subbasilare	0.036	0	**0.275**	0	na	na	na
Mniodendron comosum	**0.506**	0.053	0	0	na	na	na
Hypnodendron vitiense	0.169	0	0	0	na	na	na
Hypnum chrysogaster	0.379	0.226	0.291	0.170	-0.005	-0.005	na
Hypnum cupressiforme	0.135	0.074	0	0.207	na	na	na
Hypopterygium tamarisci	0.102	0.051	0.062	0.065	na	na	na
Lembophyllum divulsum	0.111	0	0.047	0	na	na	na
Leptotheca gaudichaudii	0.156	0.095	0.275	0.148	na	-0.002	na
Leucobryum candidum	**0.403**	0.159	0.156	0.076	na	na	na
Lopidium concinnum	0.120	0	0	0	na	na	na
Polytrichum juniperinum	0	0	0.083	**0.651**	na	na	**0.01**
Ptychomnion aciculare	0.424	0.455	*0.477*	0.132	0.002	0.001	**-0.011**
Pyrrhobryum mnioides	0.120	0	0	0	na	na	na
Racopilum cuspidigerum	0	0	**0.258**	0	na	na	na
Rhaphidorrhynchium amoenum	0.258	0.116	**0.474**	0.095	na	*0.006*	na
Rhizogonium distichum	0.159	0.081	0.239	0	na	na	na
Rhizogonium novae-hollandiae	0.350	**0.640**	0.443	0.039	0.004	-0.001	na
Rosulabryum billarderii	0.03	0.019	**0.340**	0.137	na	na	na
Rhynchostegium tenuifolium	0.292	0.244	0.218	0.076	-0.006	-0.001	na
Thamnobryum pumilum	0.120	0	0	0	na	na	na
Thuidiopsis furfurosa	0	0	0.129	0	na	na	na
Thuidiopsis sparsa	0.237	0.266	0.317	0.022	-0.005	-0.0003	na
Wijkia extenuata	0.406	0.604	**0.611**	0.114	0.005	-0.001	**-0.011**

	IndVal				Response to distance		
Species (liverworts)	Mature	~45	~27	~7	~45	~27	~7
Acromastigum colensoanum	**0.363**	0.034	0.027	0	na	na	na
Acromastigum mooreanum	0.169	0	0	0	na	na	na
Anastrophyllum schismoides	0.120	0	0	0	na	na	na
Balantiopsis diplophylla	0.123	0.094	0.139	0.079	na	na	na
Bazzania adnexa	**0.671**	0.494	0.205	0.049	-0.003	**-0.009**	na
Bazzania monilinervis	0.120	0	0	0	na	na	na
Cephaloziella exiliflora	0.006	0	0.107	**0.750**	na	na	**0.016**
Cephaloziella hirta	0	0	0.039	**0.326**	na	na	na
Cyanolophocolea echinella	0.198	0.045	0.228	0.182	na	0.005	na
Chiloscyphus latifolius	0	0	0	0.183	na	na	na
Chiloscyphus multipennus	0.103	0.145	0	0	na	na	na
Chiloscyphus semiteres	0.070	0.046	**0.399**	0.363	na	0.007	**0.007**
Chiloscyphus villosus	0	0	0.109	0.069	na	na	na
Eotrichocolea polyacantha	0.169	0	0	0	na	na	na
Frullania sp	0.209	0.072	0.062	0	na	na	na
Gackstroemia weindorferi	**0.401**	0.240	0.068	0	-0.003	na	na
Heteroscyphus billardierei	**0.267**	0	0	0	na	na	na
Heteroscyphus circumdentatus	0.120	0	0	0	na	na	na
Heteroscyphus coalitus	**0.48**	0.167	0.149	0.019	**-0.017**	na	na
Heteroscyphus cymbaliferus	0.120	0	0	0	na	na	na
Heteroscyphus fissistipus	0.439	**0.607**	0.253	0.034	0.001	-0.0004	na
Heteroscyphus limosus	0	0	0.129	0	na	na	na
Heteroscyphus knightii	0	0.082	0.100	0	na	na	na
Hymenophyton flabellatum	**0.430**	0.05	0	0	na	na	na
Isotachis intortifolia	0	0	0	0.129	na	na	na
Kurzia compacta	0.169	0	0	0	na	na	na
Lepidozia glaucophylla	0	0.129	0	0	na	na	na
Lepidozia laevifolia	**0.501**	0.23	0.081	0	-0.0002	na	na
Lepidozia ulothrix	**0.434**	0.403	0.217	0.015	**0.008**	-0.001	na
Marchantia berteroana	0	0	0	**0.258**	na	na	na
Marsupidium surculosum	**0.244**	0.032	0	0.041	na	na	na
Megaceros gracilis	0.120	0	0	0	na	na	na
Metzgeria furcata	**0.366**	0.109	0.083	0	na	na	na
Plagiochila fasciculata	**0.235**	0	0	0.024	na	na	na
Plagiochila retrospectans	0.120	0	0	0	na	na	na
Plagiochila strombifolia	**0.207**	0	0	0	na	na	na
Podomitrium phyllanthus	0.274	**0.417**	0.097	0.023	-0.005	na	na
Radula buccinifera	0.228	0.220	0.023	0	na	na	na
Riccardia aequicellularis	0.017	0.053	0.228	0.174	na	na	na
Riccardia spp.	0.227	0.121	**0.456**	0.274	0.002	0.002	-0.002
Riccardia cochleata	0.074	0.022	**0.291**	0.081	na	na	na
Saccogynidium decurvum	**0.293**	0	0	0	na	na	na
Schistochila lehmanniana	**0.473**	0.045	0.030	0	na	na	na
Symphyogyna podophylla	0.204	0.070	0.055	0.039	na	na	na
Telaranea sp.	**0.582**	0.526	0.454	0.125	-0.003	**-0.010**	**-0.024**
Treubia tasmanica	0	0	0.129	0	na	na	na
Trichocolea mollissima	**0.394**	0	0.013	0	na	na	na
Tylimanthus diversifolius	**0.491**	0.036	0.02	0	na	na	na
Tylimanthus pseudosaccatus	**0.351**	0.113	0	0	na	na	na
Zoopsis argentea	**0.503**	0.219	0.249	0.045	**-0.011**	*-0.006*	na
Zoopsis leitgebiana	**0.315**	0.058	0	0.023	na	na	na

Appendix 3

Reprint attachment of the paper published from this thesis

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